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A River Ran Through It:

Recruitment of Riparian Cottonwoods

in the Oldman River Basin

Final Report following Alberta Environmental Protection Agreement #96-0180.

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Submitted to:
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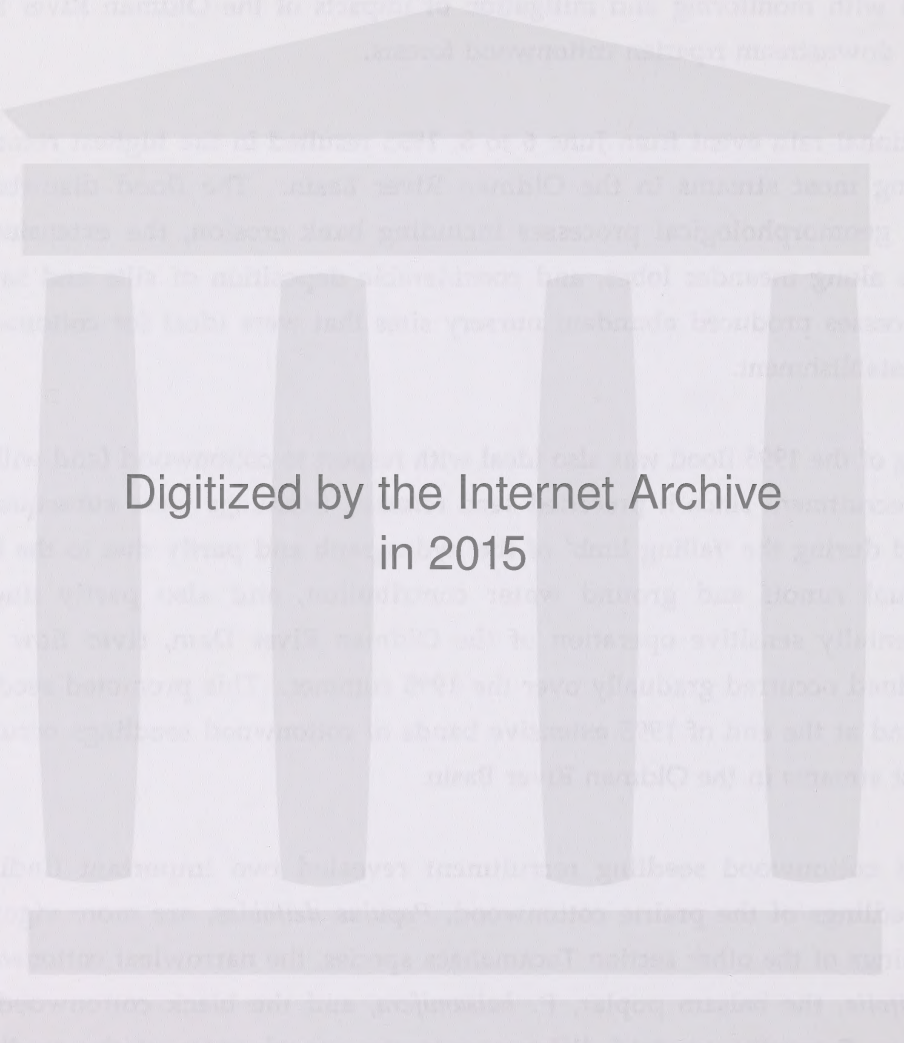
Summary

Field and laboratory studies were conducted in 1995/6 to continue investigations associated with monitoring and mitigation of impacts of the Oldman River Dam Project on downstream riparian cottonwood forests.

An exceptional rain event from June 6 to 8, 1995 resulted in the highest recorded flows along most streams in the Oldman River Basin. The flood disturbance promoted geomorphological processes including bank erosion, the extension of point bars along meander lobes, and considerable deposition of silts and sands. These processes produced abundant nursery sites that were ideal for cottonwood seedling establishment.

The timing of the 1995 flood was also ideal with respect to cottonwood (and willow) seedling recruitment since it preceded seed release. Seedlings were subsequently established during the 'falling limb' of the hydrograph and partly due to the high and gradual runoff and ground water contribution, and also partly due to environmentally sensitive operation of the Oldman River Dam, river flow and stage declined occurred gradually over the 1995 summer. This promoted seedling survival and at the end of 1995 extensive bands of cottonwood seedlings occurred along most streams in the Oldman River Basin.

Studies of cottonwood seedling recruitment revealed two important findings. Firstly, seedlings of the prairie cottonwood, *Populus deltoides*, are more vigorous than seedlings of the other section Tacamahaca species, the narrowleaf cottonwood, *P. angustifolia*, the balsam poplar, *P. balsamifera*, and the black cottonwood, *P. trichocarpa*. Secondly, ten-fold differences in the growth rates of the seedlings occurred from upstream of the Oldman Reservoir (slow growth), downstream through Lethbridge (medium growth) and on to Medicine Hat (rapid growth). These findings support the proposal that cottonwoods along foothills streams are



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less reliant on seedling recruitment (and more reliant on suckering and other forms of clonal recruitment), whereas cottonwoods in prairie regions are especially reliant on seedling recruitment.

The environmental benefit also extended downstream along the South Saskatchewan River where seedling recruitment was even more dramatic. The sustenance of the 1995 seedlings will require sufficient instream flows through the summers of 1996 and 1997. Presently favorable snow pack and ground water conditions provide promise that sufficient water will be available for cottonwoods in 1996.

Studies of cottonwood phenology (timing of bud flushing, flowering, seed release and senescence (leaf yellowing)) continued in 1995 along with systematic measurements of branch growth. These studies revealed the substantial diversity of cottonwoods along the Oldman River system and were also useful for recognizing clones, clusters of neighboring trees (ramets) that share a common root system.

DNA fingerprinting analyses using random amplified polymorphic DNA (RAPD's) were continued and a number of specific 10-nucleotide primers were identified that are useful for revealing cottonwood clones. Common DNA primers are being used by various research groups to enable comparisons of Oldman River cottonwoods with cottonwoods from other river basins.

One refereed publication was released and a second manuscript was accepted for publication in 1995. The 1995 studies will be complemented by 1996 studies to follow the success of the seedlings that were established following the 1995 flood. Additional refereed publications are anticipated in 1996 and 1997 from the 1995 studies enabled by Alberta Environmental Protection Agreement #96-0180.

Transects 1995 Summary

Cottonwood seedling recruitment following the 1995 flood was examined with the establishment of 21 permanent transects established at eight different sites along the Oldman and S. Saskatchewan rivers.

Site locations were as follows:

Oldman River

1. Animal Disease Research Institute (2 sites)

2. 509 Bridge (near Kipp)

3. University of Lethbridge grove

4. Alexander park in Lethbridge

5. Popson park in Lethbridge

6. Taber Provincial Park

South Saskatchewan River

7. Police Point Park in Medicine Hat

Methods varied somewhat, but were generally as follows:

1) A transect line was established perpendicular to the river.

2) Elevation levels were recorded along the line and notes were taken describing the general vegetation and substrate.

3) Quadrats were placed along the line at seedling bands or in areas where seedlings were established. The distance between the placement of the quadrats was dependent on the density of the seedlings in the area; the more dense the seedlings, the more quadrats taken.

4) Measurements taken of the seedlings involved:

i) counting the number of cottonwood seedlings per quadrat

ii) randomly measuring at least ten heights of seedlings within the quadrat from the base of the stem exposed from the soil to the tip of the meristem

iii) measuring the length of the longest leaf (not including petiole) on each of the seedlings.

Measurements and observations were then transcribed. Each transect has a hard copy and a backup of the following five files:

1. Elevation Data
2. Elevation Graph
3. Graph Data
4. Seedling Density Graph
5. Seedling Measurements

Attached are the averaged measurements for each transect. Three of the sites were revisited during the summer of 1995. Sites were visited through the period of July 4-September 23, 1995.

Cottonwood seedlings are established in bands. Therefore, in general, the density numbers are inaccurate because the density of the seedlings along a line varied greatly.

One might note the large variation in density at the Popson and University of Lethbridge grove sites when revisited. These are accounted for by the fact that the Popson site transects were the first to be established in my absence with slightly different methods. As well, at the U of L site, when the initial seedling densities were measured, one could not distinguish between cottonwood seedlings and other seedlings.

Andrea Kalischuk

Site	Date	Transect #	Mean Shoot Ht (mm)	Mean Leaf Length (mm)	Mean density (/m*2)
ADRI	Aug. 2	508	9.90	5.30	182
		512	15.50	11.80	477
		513	14.90	9.80	286
	Sept. 15	508	15.60	11.00	164
		512	18.30	12.60	170
		513	15.10	12.40	300
ADRI classic lob	Sept. 8	518	14.70	9.10	443
		519	14.20	11.00	377
Alexander	Aug. 29	517	30.80	19.70	168
509 Bridge	Sept. 23	520	20.70	14.60	388
		521	17.40	28.80	291
Police Point	Aug. 11	509	16.90	11.30	570
		510	35.50	19.30	1134
		511	13.90	8.50	462
	Sept. 22	509	51.30	20.90	383
		510	58.40	22.50	410
		511	44.20	24.10	103
Popson	July. 4	501	7.80	0.70	1026
		502	2.10	1.10	162
		503	1.00	0.50	241
	Sept. 7	501	25.00	16.00	136
		502	19.10	9.50	185
		503	20.40	19.10	375
Taber	Aug. 15	514	25.50	17.80	172
		515	21.50	12.60	226
		516	26.40	14.40	137

Site	Date	Transect #	Mean Shoot Ht (mm)	Mean Leaf Length (mm)	Mean density (/m*2)
UofL Grove	Aug. 2	504	14.10	14.70	362
		505	18.40	15.10	156
		506	21.90	11.50	1085
		507	7.30	5.80	1733
	Sept. 11	504	36.10	25.90	265
		505	33.40	22.20	118
		506	21.10	10.60	276
		507	23.80	12.50	187

Summary of Seedling Measurements from 1995

After the Flood: Cottonwood Seedling Recruitment in Chinook Country

The flood of June, 1995 was ideal in permitting cottonwood seedling recruitment. The timing of the flood on the Elk, Oldman, and South Saskatchewan rivers coincided with the annual release of cottonwood seeds occurring from the end of June to early July.

Seedling establishment requires:

i) barren substrate- The flood scoured vegetation and provided deposits of silt along river banks for seedling establishment.

ii) adequate water supply- The flood elevated water table levels while weather in the following months produced a drop in water stage of 2.5 cm per day allowing seedling survival.

A hypothesis was established that cottonwood seedlings vary phenotypically and genotypically across species.

An investigation was designed such that a transect of approximately 350 km was established across southern B.C. and southern Alberta. Cottonwood seedling measurements were recorded at a total of eight sites (originally, a site at Police Point Park was to be included, but the measurements available were taken early in the summer while all the other measurements were taken towards fall).

Generally, southern B.C. consists of *Populus trichocarpa/balsamifera,* and while progressing eastwards towards Medicine Hat, the predominant species becomes *P. angustifolia,* and *P. deltoides* respectively. Species were not designated while

measuring seedlings at any site, with the exception of site 6 (Pavan Park in Lethbridge) . Site 6 is unique in consisting not predominantly of one species of cottonwood, but rather of the three species mentioned above; therefore, at site 6, each seedling measured was also given a species designation.

The results of our investigation are attached.

After analysing the data, the following conclusions were drawn:

i) Cottonwood seedling heights vary with elevation; the higher the elevation, the shorter the height of the seedlings. This makes sense as at higher elevations, the temperature tends to be lower and the growing season shorter.

ii) Cottonwood seedling heights vary across species within the same elevation. At site 6, while competing in the same environment, *P. deltoides* seedlings grew the fastest followed by *P. balsamifera* and *P. angustifolia* respectively. This is consistent with the knowledge that *P. deltoides* is less capable of asexual reproduction in the form of suckering in comparison to the other cottonwood species.

Andrea Kalischuk

		Summary of Seedling Measurements from 1995							
Site	Location	River System	Elevation (m)	Distance on Transect(km)	Date 1995	Populus Species	Average Height (mm)	Standard Deviation	Standard Error
1	Fernie	Elk	825	0	8-Oct	Po T/B	25.44	8.60	1.24
2	Castle	Oldman	1197	78	31-Oct	Po T/B	8.81	2.38	0.48
3	Upper Oldman	Oldman	1208	54	31-Oct	Po T/B	8.68	1.57	0.32
4	Cottonwood B	Oldman	1036	74	16-Oct	Po T/B	25.44	8.66	1.24
5	Kipp Br.	Oldman	864	141	6-Oct	Po D/A	35.12	18.77	1.63
6	Pavan Park	Oldman	823	149	5-Oct		53.60	31.93	2.16
						Po B	46.14	23.00	3.10
						Po A	35.66	17.14	2.05
						Po D	96.86	33.91	5.73
7	Bow Island	S.Sask.	701	234	25-Oct	Po D	73.34	22.28	2.28
8	Rattlesnake	S.Sask.	653	297	10-Oct	Po D	203.80	57.74	8.09
9	Police Pt.	S.Sask.				Po D			.

Monitoring Riparian Poplar Phenology for Purposes of Clone-group Delineation

To investigate sexual versus clonal replenishment in riparian poplars, a study of phenology has been initiated. The study site being utilized was set up two years ago and it involves a man-made island in the Oldman River. The island is located directly below the University of Lethbridge campus and is defined by the weir diversion canal. All mature cottonwoods (n=390) on the island have been numbered with aluminum tags and mapped. For each tree a phenological history of the 1995 growing season was compiled. To create this view of cottonwood phenology, observations were planned to provide coverage of structural similarity, phenological similarity, and spatial association.

STRUCTURAL SIMILARITY:

1) Foliar morphology is one of the easiest, most enlightening characteristics available to classify similarity. Leaf morphology is commonly used to indicate species and hybrid composition. Since cottonwoods exhibit heterophylly, only mature leaves were collected and several leaves were measured to minimize confounding variation. The characteristics measured included; petiole length, blade length, blade width, marginal tooth depth, distance from base of blade to point of maximum blade width, and angle of blade edge from petiole. The leaves from this study site fall into eight distinguishable morphological categories. Three of these categories correspond to the parental species types; *Populus angustifolia*, *P. balsamifera*, and *P. deltoides*. The other five categories represent combinations of hybrid origin (simple crosses between all three species and complex backcrosses involving hybrids also occur naturally)

2) Trunk architecture is an easily observable characteristic in mature cottonwoods. Variation in characteristics such as branching form and stature is partially species dependent, the remainder is an indication of environment and individual variation. Age-related differences in trunk architecture were minimized by only comparing individuals of

similar maturity and size.

3) Eriophyid mites colonize cottonwood branches and induce diagnostic gall formation. These mites are thought to be distributed widely throughout the riparian system, and given the long life span of individual cottonwoods, it is thought that all such mature trees have been exposed to the mites at one time or another. For these reasons, the relative abundance of galls on a tree should indicate the degree of that tree's susceptibility or resistance to infestation. The abundance of mite galls can be assessed most easily in the winter months before the leaves emerge. The number of galls surveyed in a specific, limited amount of time gives an indication of relative abundance on a particular tree.

4) Cottonwoods are dioecious; a given individual can only be either male or female. The sex of the tree is only apparent in the very early spring at the time of flowering. Flowering usually commences in early May. At this time, differences in the flowers are easily observable using binoculars. The most prominent distinguishing feature is that the male flowers appear red while those of the female are green. As the flowers mature many other sexual differences become obvious. When the female catkins finally mature, their capsules ripen and rupture, releasing large numbers of seeds with their associated 'cotton'. This display enables the recognition of female cottonwoods farther into the growing season.

PHENOLOGICAL SIMILARITY:

1) The timing of flowering is a function of environment and genotype. Since the trees of this study site share a very specific elevation and photoperiod, variation due to the environment is unlikely. By recognizing differences in age and health the remaining variation is attributable to species and individual variation. For every tree on the site, the date of flowering initiation, and the progress of flower-expansion/development was followed on a semi-daily basis for the month of May, 1995.

2) The timing of leaf flush is much like that of flowering; the same conventions apply as mentioned above. The date of bud break and the progress of leaf expansion was observed

synchronously with the flowering observations since both groups of events were mainly simultaneous.

3) The timing of leaf senescence in the autumn was also observed with the same conventions applying. In this case, the pattern and rate of leaf-yellowing, and the degree and rate of leaf-drop were coded for comparison. These observations began in late September and ran on into October,1995.

SPATIAL ASSOCIATION:

Finally, the spatial association of cottonwood trunks to each other was investigated. Using maps produced in the summer of 1994, all of the trees on the site were digitized. In this way X-Y coordinates were assigned to each tree. These coordinates were translated into a meter-based equivalent. From this information it was then possible to calculate the distances of every tree from every other tree. After extensive data manipulation, the neighboring trees of similar sex and species within 20 meters or less, for every tree were compiled. These lists of neighbors represent potential clonal associations and will be further delineated according to the remaining phenological characteristics.

Lori A. Gom

DNA Fingerprinting of Riparian Cottonwood to Detect Clonal Recruitment

INTRODUCTION.

A unique hybridization complex largely located in the Oldman River Valley near Lethbridge is formed by the four species of *Populus* (poplar or cottonwood) native to southern Alberta. A consequence of free gene flow amongst the different poplar species has lead to the formation of numerous hybrids which has lead to ambiguous identification. Phenological and morphological characteristics including leaf flushing period, senescence timing and leaf characters such as general shape, margin type and dentation pattern are useful for *Populus* species identification (Rood et al., 1986). Furthermore, gas chromatographic-mass spectrometric analyses of *Populus* bud exudates has also revealed distinct differences in overall biochemical profiles between the species (Greenaway et al., 1991).

Poplars have two primary reproduction strategies: (1) sexually through the production of seeds, and (2) asexually through the formation of adventitious shoots from the roots. Seedlings produced as a result of gamete recombination will have a genetic compliment that is reflective of both parental donors, thus enabling genetic diversity. Those individuals produced from root suckering will have an identical genetic compliment to the single parent. Phenological and morphological characteristics may not be significantly distinct between closely related juvenile individuals and thus an alternative means of discriminating between asexually and sexually generated individuals would desirable. The recent development of the polymerase chain reaction (PCR) to amplify DNA, and the use of randomly amplified polymorphic DNA (RAPD) has resulted in a potentially useful tool for clonal identification in poplar.

METHODS AND MATERIALS.

Seeds were collected June 22, 1995, from female *Populus* trees whose classification status had previously been determined using morphological measures. Since the matings were not controlled, these seeds are considered at worst half-siblings. Seeds were germinated on water saturated filter paper lining Petri dishes. Seedlings were maintained for up to 1 week in the Petri dishes and then transplanted into Metro-mix filled pots incubated in the University of Lethbridge greenhouse. Young leaves from the main shoot tip axis of 10 individuals from *P. deltoides* (parental ID# 347 and 134) and *P. balsamifera* (ID #19-26) saplings were harvested and frozen in liquid nitrogen until DNA extraction.

DNA was extracted from approximately 2 g of leaf tissue using the method of Doyle and Doyle (1990). Precipitated DNA was hooked using a glass rod, rinsed several times in ethanol (70%)/sodium acetate (10 mM) and resuspended in RNAse buffer (10mM Tris and 15mM NaCl, pH 7.5). Following the addition of RNAse A was added to yield a final concentration of 10 µL/mL, the samples were incubated at 37°C for 30 min and then reprecipitated. The DNA was washed in an ethanol/ sodium acetate solution, dried under vacuum and resuspended in water.

Techniques for the generation of RAPD markers are well documented (Rafalski et al., 1991). Primers from the 200 decamer series were obtained from J. Carlson, University of British Columbia (UBC) and were used singly in each reaction (Table 1). The final reaction mixture included 10X PCR reaction buffer (Saiki, 1990), 10 mM $MgCl_2$, 1.25 mM dNTP (deoxyribonucleoside 5'-phosphates), 2.0 µM primer, 1 unit of *Taq* polymerase, 50 - 100 ng genomic DNA made to a final volume of 25 µL with sterile double-distilled water. Amplification of the DNA was carried out using a Perkin Elmer Geneamp 9600 thermocycler programmed for 45 cycles of 1 min at 94°C (denaturation), 1 min at 35°C (annealing) and 2 min at 72°C (extension), 1 cycle of 1 min at 94°C, 1 min at 35°C and 10 min at 72°C and a final soak at 14°C.

The RAPD products (3 µL) plus loading buffer (3 µL of a mix of bromophenol blue/glycerol) were resolved by electrophoresis using 1.2% agarose in 1X TAE buffer. A 1 kb ladder was included as a size marker and the bands detected with ethidium bromide staining [2.5µL (10 mg/mL)/100 mL].

RESULTS AND DISCUSSION.

RAPD analysis involves the amplification of DNA segments using random primers, generally of ten bases (decamers), to detect polymorphic regions within the genome that are delineated by the specific primer sequence. The products generated by PCR are separated by agarose gel electrophoresis and reveal sequence variation in the form of variable numbers of bands of variable length which may be characteristic of species and/or individuals. The presence or absence of a band is evaluated and the data subjected to statistical analysis; no previous sequence information is required for the individual.

Of the 14 different UBC decamer primers amplified with the *P. deltoides* (ID# 347) genomic DNA, 3 primers (ID# 283, 285 and 295) showed evidence of polymorphisms between different individuals (Table 1). Examples of polymorphic bands used for discrimination within individuals from the #347 *P. deltoides* sample are shown in Figure 1.

Collectively, the three primers generated a total of 22 clear, easily detectable bands, 16 of which were polymorphic among the individuals of *P. deltoides* (347). Easily detectable, well-resolved bands were those that were reproducible over repeated runs, with sufficient intensity to determine the presence or absence in samples with the same relative band intensity. Other polymorphic primers produced patterns that were either faint and hard to detect or not reproducible. The total number of bands produced per primer varied from 4 to 10. The size of the bands ranged from 500 to 1700 base pairs (bp) (Fig. 1). The three primers (283, 285 and 295) were selected

for further evaluation using DNA extracted from other *P. deltoides* (134) individuals and a different poplar species, *P. balsamifera* (19-26).

Following careful selection of primers, it appears that RAPD techniques offer a reliable method for individual identification of poplars. Future studies should include: (1) extraction of DNA from *P. angustifolia*, (2) determination of additional primers capable of generating polymorphic banding patterns, (3) generation of a data matrix from banding pattern evaluation and cluster analysis to determine the similarity among samples and (4) amplification of DNA extracted from clonally propagated cuttings using the selected primers and analysis of the banding pattern produced.

Karen Zanewich

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Table 1. Nucleotide sequences of UBC primers used for initial RAPD screening of *P. deltoides* (347) genomic DNA.

UBC primer number	Nucleotide sequence produced	Amplification result
256	TGC AGT CGA A	none
259	GGT ACG TAC T	none
267	CCA TCT TGT G	banding*
268	AGG CCG CTT A	none
270	TGC GCG CGG G	none
281	GAG AGT GGA A	banding*
283	CGG CCA CCG T	polymorphisms
285	GGG CGC CTA G	polymorphisms
286	CGG AGC CGG C	banding*
290	CCG CGA GCA C	none
292	AAA CAG CCC G	banding*
293	TCG TGT TGC T	banding*
295	CGC GTT CCT G	polymorphisms
296	CCG CTG GGA G	none

* banding pattern detected but bands produced are of poor quality or not reproducible.

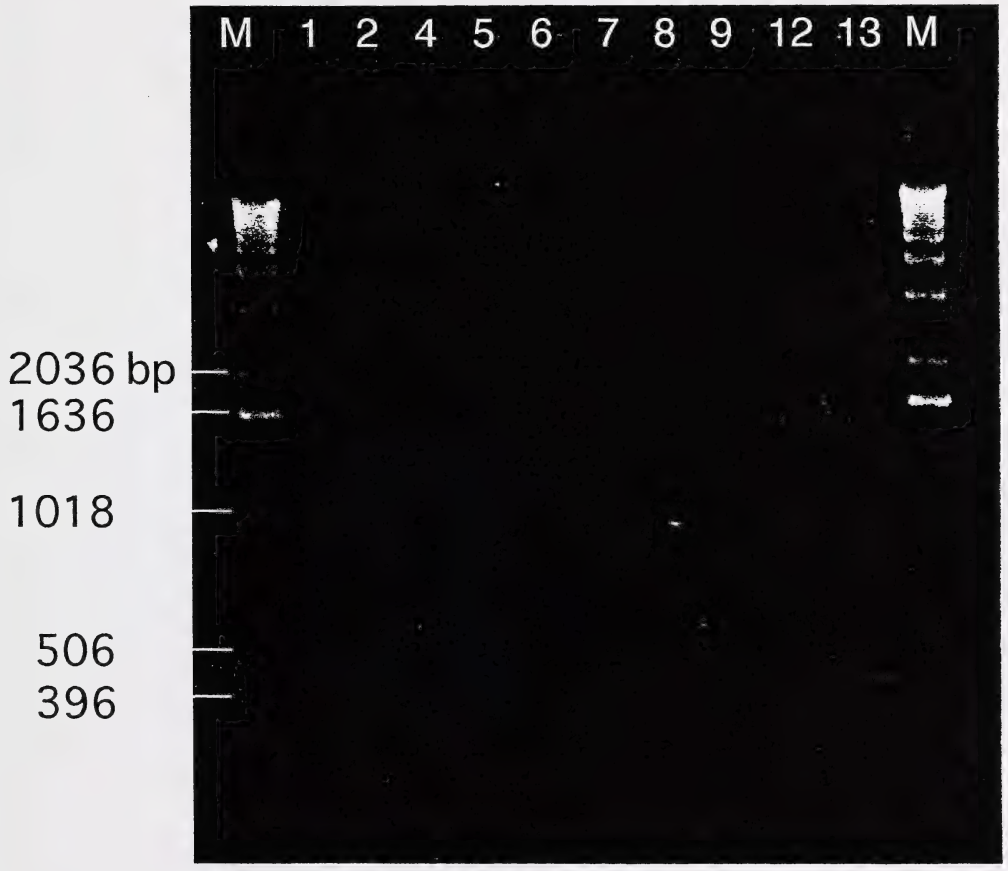

Figure 1. RAPD profiles of DNA from individuals of *Populus deltoides* (347) using UBC primer 295. M, 1Kb DNA ladder.

Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta

Stewart B. Rood, John M. Mahoney, David E. Reid, and Leslie Zilm

Abstract: Completed in 1951, the St. Mary Dam enables water storage and diversion for irrigation; river flows downstream are consequently dramatically reduced during summer months. To assess historical changes in the abundance of riparian cottonwoods (*Populus balsamifera*, *Populus angustifolia*, and a few *Populus deltoides*), airphoto analyses were conducted for 40-km river reaches upstream and downstream from the dam and along adjacent dammed and undammed rivers. Cottonwoods along the lower St. Mary River are confined by steep-walled canyons to narrow bands and consequently analyses of the lineal river distance associated with cottonwoods were conducted. These revealed a 68% decline from 1951 to 1985. The decline was progressive, with 28.9, 27.6, 15.1, and 7.6% of the reach associated with cottonwoods in 1951, 1961, 1981, and 1985, respectively. Ground surveys from 1985 to 1994 indicated further decline after 1985 and an absence of cottonwood seedlings and saplings. Cottonwood stands upstream from the St. Mary Dam and along adjacent rivers are more extensive and analyses of the areal extent of stands were consequently appropriate. These indicated minor change along the upper St. Mary (−0.5%), the upper (+1.9%) and lower Waterton (+3.5%), and the upper Belly (−9.1%) rivers, and an increase in forest abundance along the lower Belly River (+52.2%), between 1951 and 1985. Thus, the decline of cottonwoods along the lower St. Mary River was not symptomatic of a general pattern of decline in the region. Analyses of historical stream flows indicated that the cottonwood mortality was drought induced as a result of insufficient flows during the hot, dry summer periods and abrupt flow reductions following the high-flow period in the late spring. The riparian water table was determined to be closely coordinated with river stage, as changes in river elevation were followed by quantitatively similar changes in water table depth. Along the St. Mary River, reduced sedimentation downstream from the dam was not considered to be responsible for the cottonwood decline. The historically sparse cottonwood abundance along the lower St. Mary River may have reflected environmental conditions that were naturally only marginally suitable, and those groves may have been particularly vulnerable to the impacts of river flow regulation.

Key words: *Populus*, cottonwoods, instream flows, mortality, riparian vegetation.

Résumé : Complété en 1951, le barrage St-Mary peut accumuler l'eau et servir de diversion pour l'irrigation; l'écoulement de l'eau en aval est conséquemment fortement réduit pendant les mois d'été. Pour évaluer les changements historiques de l'abondance des peupliers riparien (*Populus balsamifera*, *Populus angustifolia* et quelques *Populus deltoides*), les auteurs ont analysé les photos aériennes des 40 km de rivière en amont et en aval du barrage ainsi que le long de rivières adjacentes portant ou non des barrages. Le long de la partie inférieure de la rivière St-Mary les peupliers sont confinés, par des falaises escarpées, à d'étroites bandes et, conséquemment, les auteurs ont étudié la ligne équidistante de la rivière où se trouvent les peupliers. On y observe un déclin de 68% entre 1951 et 1985. Le déclin est progressif avec 28,9, 27,6, 15,1 et 7,6% de l'étendue associée aux peupliers respectivement en 1951, 1961, 1981 et 1985. Des suivis au sol de 1985 à 1994 indiquent que le déclin s'est poursuivi après 1985 et que les semis et plantules de peupliers sont totalement absents. Les peuplements de peupliers en amont du barrage St-Mary et le long des rivières adjacentes sont plus étendus et il convenait d'effectuer l'analyse des surfaces. Ces analyses montrent des changements mineurs en amont sur la rivière St-Mary (−0,5%), en amont (+1,9%) et en aval (+3,5%) sur la rivière Waterton, ainsi qu'en amont (−9,1%) sur la rivière Belly, et une augmentation de l'abondance de la forêt (52,2%) sur

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l'aval de la rivière Belly, entre 1951 et 1985. Ainsi, le déclin des peupliers le long de la rivière St-Mary ne constitue pas un patron général de ce déclin dans la région. Les analyses historiques des cours d'eau indiquent que la mortalité des peupliers est induite par la sécheresse causée par l'écoulement insuffisant pendant les périodes chaudes et sèches de l'été et les brusques réductions de l'écoulement suivant les forts écoulements de la fin du printemps. On a constaté que la nappe phréatique riparienne est étoitement reliée avec la hauteur de la rivière, puisque des changements dans l'élévation de la rivière sont suivis de changements quantitativement similaires dans la profondeur de la nappe phréatique. Le long de la rivière St-Mary, on ne peut considérer qu'une réduction de la sédimentation à partir du barrage pourrait être responsable du déclin des peupliers. La faible présence historique des peupliers le long de la rivière St-Mary pourrait refléter des conditions environnementales qui étaient naturellement marginales pour ces espèces et ces canyons étaient probablement vulnérables aux impacts de l'écoulement de l'eau.

Mots clés : *Populus*, les peupliers, l'écoulement, la mortalité, la végétation riparienne.
[Traduit par la rédaction]

Introduction

Riparian (river flood plain) cottonwood forests provide environmental, aesthetic, and recreational relief in many otherwise treeless regions of North America's western prairies and Rocky Mountain foothills. Riparian woodlands often comprise the regions' richest wildlife habitats, offering forage, cover, and reproduction sites for numerous birds and mammals (reviewed in Finch and Ruggiero 1993). Generally less than 2 km wide, the cottonwood forests can extend for tens or hundreds of kilometres in length and link the prairie, foothills, and mountain ecosystems, enabling wildlife and plant movements.

As well as being particularly valuable, riparian cottonwood forests are also particularly vulnerable. Riparian areas offer desirable sites for crop or livestock production, domestic settlement, transportation corridors, and other uses that involve forest clearing and (or) lead to a failure of cottonwood recruitment. River damming and water diversion, principally for irrigation, are common in the semiarid regions of western North America, and such damming has led to downstream forest decline along numerous rivers (reviewed in Rood and Mahoney 1990, 1993). It is very likely that the downstream impacts of damming are primarily dependent on the patterns of river flow management and consequently an understanding of the relationships between river flow patterns and the responses of riparian cottonwoods are important. Such understanding may be achieved by analyses of river flows and riparian cottonwoods along various dammed and undammed rivers.

The abrupt decline of riparian cottonwoods downstream from the St. Mary Dam was previously introduced and possible causes for decline have been proposed (Rood and Heinze-Milne 1989). The present study continued investigations of the cottonwoods along the St. Mary and adjacent rivers with two objectives: (*i*) to assess the pattern of decline over time, and (*ii*) to clarify the causes of the forest mortality. Particular attention was directed towards the relationships between river flow and cottonwood condition, since these relationships are crucial for the sustenance of phreatophytic riparian woodlands (Hughes 1994; Mahoney and Rood 1991*b*, 1992; Rood and Heinze-Milne 1989; Scott et al. 1993; Stromberg and Patten 1991, 1992).

Materials and methods

Background: the St. Mary River

The St. Mary River originates in alpine tundra in the Lewis Range of the Rocky Mountains in Glacier Park, Montana (maps showing the study region are included in Rood and Heinze-Milne 1989 and Rood et al. 1995). Numerous alpine streams flow into Upper St. Mary Lake, from which the St. Mary River flows to Lower St. Mary Lake and then northward from Montana into Alberta. A diversion weir is situated near the outflow of Lower St. Mary Lake and diverts some water to the Milk River for its return through Alberta back to Montana.

In Alberta, the largest tributaries of the St. Mary River are Lee Creek, a free-flowing tributary that originates from the eastern border regions of Glacier and Waterton parks, and Pothole Creek, which flows into the St. Mary River near the confluence with the Oldman River. Pothole Creek delivers irrigation return flows during the summer months and is situated upstream from the lower St. Mary River hydrometric gauging station. During the summer months, up to one-half of the flow of the lower St. Mary River results from this contribution and, consequently, the summer discharge data presented in the figures of the present paper are sometimes considerably higher than the flows through the river reach along which cottonwoods were studied. Higher flows are proportionally less influenced by Pothole Creek, and thus the peak flow patterns are representative of flows through the principal cottonwood study reach along the lower St. Mary River.

Analyses of historical cottonwood abundances

Analyses of historical cottonwood (primarily balsam poplars, *Populus balsamifera* subsp. *balsamifera*, and narrowleaf cottonwoods, *Populus angustifolia*, with a few prairie cottonwoods, *Populus deltoides*, and various interspecific hybrids; Greenaway et al. 1991; Rood et al. 1986) abundances along the St. Mary River involved a lineal ticking method described previously (Rood and Heinze-Milne 1989), using two sets of black and white airphotos: July 1951 (scale 1 : 40 000) and June 1985 (1 : 30 000). This lineal analysis involved tracing of the rivers on transparencies, marking the river maps at 1-mm intervals and determining whether

cottonwood groves occurred on either bank for each 1-mm segment. This method determines the proportion of river length associated with riparian cottonwoods and is thus a one-dimensional simplification of cottonwood abundance. This approach is appropriate for the lower St. Mary River, since those cottonwoods are restricted to narrow bands along a flood plain that is confined by steep coulees and sandstone cliffs.

Two-dimensional areal analyses of historical cottonwood abundances in 1951 and 1985 were conducted for the St. Mary River and for the adjacent Belly River, upstream and downstream of the Belly River weir, and for the Waterton River, upstream and downstream of the Waterton Dam. For areal analyses, photographic enlargements were made from 1951 and 1985 airphotos to produce 1 : 15 000 photomosaics. Cottonwood stands were outlined, and areas were determined by computerized digitization.

For both lineal and areal analyses, complete river reaches were assessed, extending 40 km upstream and downstream from reservoirs or the Belly River weir. Thus, all forest stands along these reaches were quantified rather than applying an experimental design involving subsampling and the subsequent extrapolation to a larger population and corresponding statistical evaluation.

Field inventories

About 100 visits to the St. Mary River were made from 1983 to 1994, including three low-altitude (150 m) flyovers, and field visits by vehicle and canoe. Field visits particularly investigated the occurrence of young seedlings or saplings, the apparent health of mature trees, and the occurrence of sand and silt bars along meander lobe point bars or along lateral bars.

Analyses of historical stream flow

Historical stream-flow data for the St. Mary River had been collected by the Water Survey of Canada from hydrometric gauging stations 05AE027, at the International Boundary, and 05AE006, at the bridge between Lethbridge and Standoff. Daily mean hydrographs were compared for upstream versus downstream survey stations for each year from 1951 through 1993, with particular consideration for abrupt reductions of flow and extended periods of minimum flows during the summer months. Maximum daily mean discharges were analyzed by flood-recurrence analyses for the period from 1960 to 1990 using the following formula:

$$[1] \quad T = \frac{n+1}{m}$$

where T is the return interval in years, n is the total number of years considered, and m is the order of flow events, beginning with the largest event as 1.

Analyses of riparian water table level

In June 1993, transects with six piezometer tubes (wells), each consisting of a 4 m long × 4 cm internal diameter slotted PVC pipe, were installed at each of two sites along the lower St. Mary River. The Welling Ford site is situated 39 km downstream from the St. Mary Dam at a broad meander lobe that supported a dense cottonwood grove in 1950 and still supports about 15 trees, principally balsam poplars and narrowleaf cottonwoods. The Russell Farm site is located 86 km downstream from the St. Mary Dam and is downstream from the inflow of Pothole Creek. A grove of narrowleaf cottonwoods and balsam poplars continues to survive at the Russell Farm site. Transects extended perpendicular from the river's edge and were positioned near the centre of meander lobes that sloped gradually from the river's edge. These meander lobes would be considered prime zones for cottonwood seedling replenishment. The piezometer tubes were installed with a drill truck that augered a 20 cm diameter hole 5 m deep. A hollow centre in the auger shaft permitted positioning of the piezometer tube, after which the auger was reversed for withdrawal. Water table depth measurements were made by dropping a weighted string to the water surface and string measurement after withdrawal. Repeated measurements indicated that this procedure provided readings that were precise to about 2 mm. Measurements of water table depth along the two transects were made weekly during July and August 1993 and from May through September 1994.

Analyses of proposed future operating plans

In conjunction with analyses of the proposed operations plans for the Oldman River Dam (Mahoney and Rood 1993), hydrological modelling was conducted for all rivers in the Oldman River Basin (Alberta Environment 1989*a*, 1989*b*). The modelling generated (*i*) naturalized weekly mean flows that would have occurred if no dams or diversion occurred, and (*ii*) projected flows that would follow the commissioning of the Oldman River Dam and increased diversion for irrigation and other uses up to a level recommended by present provincial policies. This proposed operations strategy was identified as ODO5 (Oldman Dam Operations 5). The modelled hydrographs were generated for stream inflow conditions that actually occurred for each of the years from 1967 to 1986 and were compared to actual historical hydrographs, averaged on a weekly time-step for comparison. Thus, three hydrographs were compared for each year, representing (*i*) modelled free flow conditions that would have occurred with no damming or diversion; (*ii*) modelled proposed flow patterns that would accompany the implementation of the strategy that is presently being applied to the South Saskatchewan River Basin; and (*iii*) actual flow patterns that occurred with the historical levels of damming, diversion, and other flow alterations.

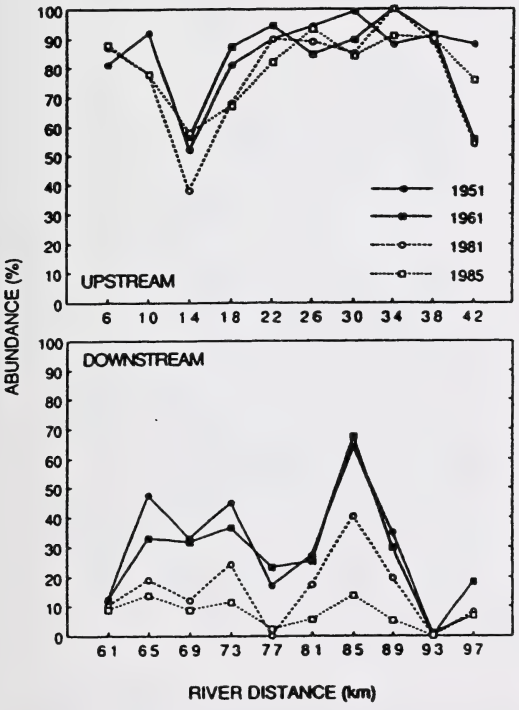
Results and discussion

Analyses of historical cottonwood abundances

Analyses of the abundance of cottonwoods along the reach downstream from the St. Mary Dam confirmed and extended the pattern previously reported (Rood and Heinze-Milne 1989). The abundances of riparian cottonwoods were consistently and progressively reduced in 8 of the 10, 4-km river reaches from 1951 to 1985 (Fig. 1). In the other 2 reaches (Fig. 1, 77 and 93 km), cottonwoods were already sparse or absent in 1951 and unchanged thereafter. Field surveys from 1985 through 1990 indicated continuing decline, and by 1990 most of the river reaches were almost void of cottonwoods.

The decline of cottonwoods progressed relatively steadily

Fig. 1. Riparian cottonwood forest abundance along ten 4-km river segments upstream and downstream from the St. Mary River Dam. These values represent the percentage of reach length associated with riparian forests on either river bank and were determined from airphotos taken in the years indicated. The values for 1961 and 1981 are reproduced from Rood et al. (1989, Fig. 2), but river distances are from the Canada – United States border rather than the St. Mary Reservoir.



between 1951 and 1985 (Fig. 2), although mortality may have been accelerated over time and particularly after 1981. This possible acceleration of mortality might reflect cumulative physiological stress, although increases in water withdrawals for irrigation also occurred between 1951 and 1981. The progressive mortality suggests that the stresses were cumulative over time and that cottonwood mortality does not include a specific lethal stress threshold that is uniform across trees and and forest groves. This conclusion is consistent with the observed progressive decline of riparian cottonwoods along various North American rivers during the severe natural drought of the 1930s (Albertson and Weaver 1945). The cumulative and progressive nature of the decline of cottonwoods along the lower St. Mary River argues that simple instream flow needs (IFN) assessments that attempt to assign a single minimum flow standard are misguided. Riparian cottonwoods may survive insufficient flows for a few years but cumulative stresses would be expected to lead to gradual mortality.

The apparent rate of cottonwood decline along the lower St. Mary River between 1951 and 1985 was about 1% per

Fig. 2. Riparian cottonwood forest abundances vs. year for four 8-km river segments downstream from the St. Mary River Dam. These values were determined from Fig. 1, with two adjacent river segments combined for each 8-km segment shown here.

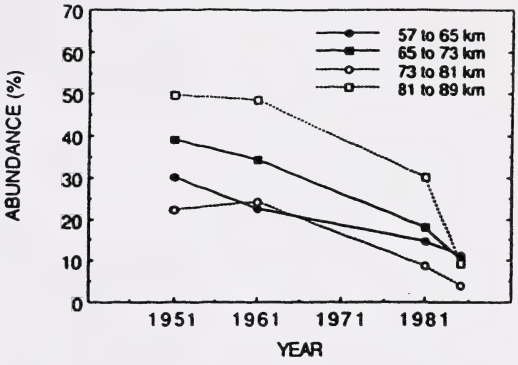
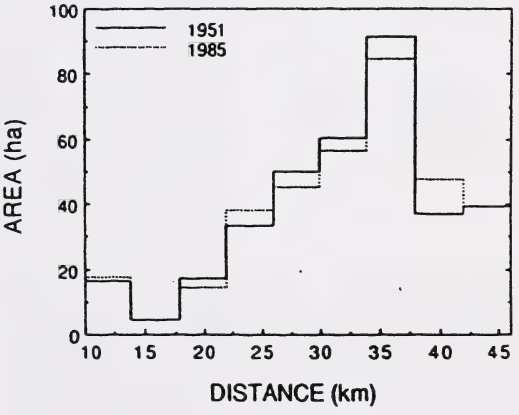


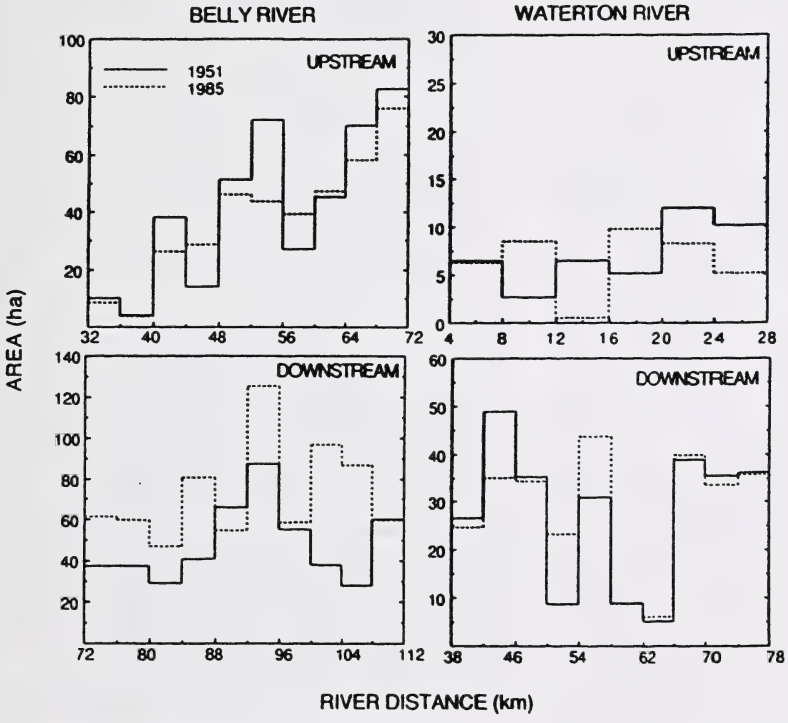
Fig. 3. Areas of riparian cottonwood forests along nine 4-km river segments upstream from the St. Mary River Dam as determined from airphotos taken in 1951 and 1985. River distances are from the Canada – United States border.



year (on an absolute basis). This is of similar magnitude but slightly slower than the 2% decline per year that Snyder and Miller (1991) reported for the Arkansas River downstream of the Colorado border. Either rate of decline is abrupt relative to the life-span of cottonwoods, which is typically about a century but may extend up to 250 years in southwestern Alberta (Shaw 1976). This rapid rate of decline would very probably not be caused solely by a failure of cottonwood replenishment and a decline of mature trees through normal aging and mortality. Instead, the abrupt decline probably represents artificially accelerated mortality between 1951 and 1985.

In contrast to the severe decline along the lower St. Mary River, lineal analyses of the St. Mary River upstream of the St. Mary Dam demonstrated little change in the abundance of riparian cottonwoods from 1951 to 1985 (Fig. 1). This apparent lack of change in forest abundance as determined by

Fig. 4. Areas of riparian cottonwood forests along 4-km segments of the Belly or Waterton rivers as determined from airphotos taken in 1951 and 1985. All distances are from the Waterton National Park boundary, with the upstream reaches being in the free-flowing sections upstream from the Belly River weir or Waterton River Dam and the downstream reaches being downstream from those control structures. Note that *y*-axis scales vary across the graphs.



the lineal analysis is consistent with the pattern previously reported for 1961 versus 1981 (Rood and Heinze-Milne 1989) (Fig. 1).

However, the assessment of lineal distance associated with cottonwoods is somewhat inappropriate for most segments of the upper St. Mary River, where broad cottonwood stands occupy the broad flood plain. Lineal assessment is applicable to segments such as Coal Canyon (Fig. 1, km 14), where like much of the lower St. Mary River, cottonwoods are limited by steep-walled canyons to narrow bands. For these upstream canyons, lineal analysis revealed little change in the distribution of cottonwoods, indicating that cottonwood decline did not occur for all narrow cottonwood groves along the St. Mary River between 1951 and 1981. This further indicates the localized loss of cottonwoods downstream from the St. Mary Dam.

Since the cottonwood stands along the upper St. Mary River generally involve large groves, historical analyses of areal extent are more appropriate than lineal analyses. The areal extent of cottonwoods was almost unchanged between 1951 and 1985 (overall decline of 0.5%), as the apparently slight increases and decreases were balanced over the 9, 4-km segments (Fig. 3). Although somewhat inappropriate, analyses of changes in areal extent were also performed for the narrow cottonwood bands downstream from the St. Mary Dam and suggested a 61% decline, a value that was quantitatively similar to that of the lineal analysis. Thus, two quantitative analyses were performed and compared. Both analyses resulted in similar conclusions regarding the St. Mary River, indicating little change upstream from the dam but major decline downstream. This indicates that the cottonwood decline downstream from the St. Mary Dam was not part of a widespread cottonwood decline such as occurred during the extensive natural drought of the 1930s (Albertson and Weaver 1945).

To further investigate possible regional patterns, historical cottonwood abundances along the adjacent Belly and Waterton rivers were conducted using 1951 and 1985 airphotos and both lineal and areal analyses. Although some localized changes occurred, total areas occupied by cottonwoods along the upper Belly River (9.1% decrease) and upper (1.9% increase) and lower (3.5% increase) Waterton River were very similar in 1951 and 1985 (Fig. 4). The relatively unchanged area of cottonwoods along the lower Waterton River contrasts slightly from an apparent decline that was observed by lineal distance analyses of airphotos taken in 1961 and 1981 (Rood and Heinze-Milne 1989). A separate lineal distance analysis conducted in the present study also indicated a slight decline of about 9% from 1951 versus 1985 airphotos. Thus, certain groves along the lower

Waterton River probably lost cottonwoods between 1951 and 1985, but changes in areal abundance were minor and compensated by increases in abundance in other groves (Fig. 4). Cottonwood groves are substantial along the lower Waterton River and consequently the areal analysis is more appropriate than the lineal distance assessment. In contrast to the St. Mary River situation, the lineal and areal analyses produced slightly different results for the lower Waterton River, emphasizing the need to select an assessment method that is suited to the riparian situation under study.

Although the areal analyses indicated little change in cottonwood abundance along the lower Waterton River between 1951 and 1985, field surveys in 1988 through 1991 revealed considerable branch and crown dieback and numerous decrepit cottonwood groves. Thus, the riparian cottonwoods are not thriving downstream from the Waterton Dam, but their overall abundance has not been substantially reduced yet.

Along the lower Belly River, cottonwood forests increased substantially between 1951 and 1985 (Fig. 4). This supports the pattern previously based on lineal distance analysis (Rood and Heinze-Milne 1989). The lower Belly River is adjacent to the lower St. Mary River, and the difference in the recent fate of the stands along these two streams further indicates that the decline along the St. Mary River is due to localized impacts, a conclusion that supports the proposal that the decline is at least partly caused by the operation of the St. Mary Dam. However, the increase in cottonwood abundance along the downstream, but not upstream, reaches of the Belly River also indicates that stream-specific and even reach-specific patterns occur with respect to cottonwood population dynamics. This localized variation complicates interpretation based solely on historical abundance and emphasizes the need to supplement airphoto inventories with field studies and physiological investigations.

Influence of changes to sedimentation patterns

The decline of riparian cottonwoods along the lower St. Mary River suggests a negative impact from some physical alteration caused by the operation of the St. Mary Dam. Two principal physical impacts have been proposed to be responsible for forest decline downstream from other dams: changes to sedimentation patterns, and alterations to patterns of stream flow (Rood and Mahoney 1990, 1993).

Changes to sedimentation patterns result from the settling out of suspended material in the slow-moving reservoir and the resultant impoverishment of the silt load downstream. This impact has been referred to as the silt shadow, cannot be easily mitigated, and is thus of particular concern with respect to river resource management. In the earlier report regarding cottonwood decline downstream from the St. Mary Dam, the lack of recovery of cottonwoods over distance downstream from the St. Mary Dam was interpreted as evidence opposing a major role of the silt shadow in the observed decline (Rood and Heinze-Milne 1989). Impacts due to the silt shadow would be most severe near the dam and would progressively attenuate downstream as the silt load recovered. In contrast, the loss of cottonwoods was consistently observed along the study segments that extended 40 km downstream (Fig. 2). Five other lines of evidence support this interpretation, further indicating that the silt-shadow effect is not responsible for the riparian cottonwood decline downstream from the St. Mary Dam.

First, the observed cottonwood decline probably involved an accelerated mortality of cottonwoods rather than being caused by a lack of cottonwood replenishment. Airphoto analyses would only assess large trees, and consequently the observed decline involved a loss of mature trees. In contrast it would be principally a failure of seedling recruitment that would be impacted by changes in downstream sedimentation patterns. However, having reached this conclusion, field surveys revealed very few seedlings and saplings along the lower St. Mary River, and consequently a failure of replenishment is occurring in addition to accelerated mortality of established trees. The failure of recruitment was probably at least partly due to drought stress: flow conditions that would lead to mortality of mature trees would even more certainly lead to mortality of vulnerable seedlings that rely on much smaller root systems.

Second, the recovery of suspended silt probably occurs rapidly downstream from the St. Mary Dam. The lower St. Mary River is relatively steep in gradient and flows swiftly past actively slumping coulees and numerous banks with thick layers of sands and silts. Field visits revealed frequently turbid waters downstream from the dam due to the abundance of suspended material. Consistent with these observations, abundant freshly deposited sand and silt bars were regularly observed after high flow periods.

Third, although the prairie cottonwood, *P. deltoides*, may prefer or require fine sand or silt substrates, the narrowleaf cottonwood, *P. angustifolia*, and the balsam poplars, *P. balsamifera*, thrive along rivers in the Rocky Mountain foothills which have very coarse substrates. These trout streams are generally clear flowing, since they are naturally impoverished of suspended sediment. Extensive balsam poplar groves exist along headwater streams in southern Alberta that flow over substrates of coarse gravel and cobbles. Balsam poplars and narrowleaf cottonwoods are the predominant species along the St. Mary River, and these species are well adapted to coarse substrates.

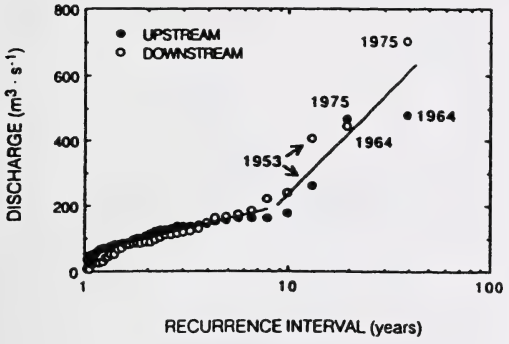
Fourth, natural lakes will act in the same capacity as artificial reservoirs in slowing the downstream flow and allowing suspended sand and silt to settle. Balsam poplars and narrowleaf cottonwoods occur immediately downstream of natural lakes in southwestern Alberta and northern Montana. For example, these trees thrive at the outflow of Upper St. Mary Lake, where the stream bed and banks consist of coarse gravel and cobble and the river is seldom turbid.

Finally, the impacts of river damming on downstream cottonwoods are not universal. Riparian vegetation has increased downstream from some dams (Johnson 1994; Williams and Wolman 1984) while cottonwood decline is observed downstream from others (reviewed in Rood and Mahoney 1990, 1993). The present study indicates that the St. Mary and Waterton dams have had different impacts, at least in terms of the immediacy of decline downstream.

Analyses of historical stream flows

The second type of physical impacts downstream from dams involves alterations to the patterns of stream flow. Most researchers have concluded that these impacts are directly or indirectly responsible for cottonwood decline downstream

Fig. 5. Peak flow recurrence (return) intervals for the St. Mary River upstream (●) and downstream (○) of the St. Mary River Dam, based on maximum daily mean discharges from 1952 to 1990, excluding 1961. Approximate fit lines are plotted to reflect a two-component function.



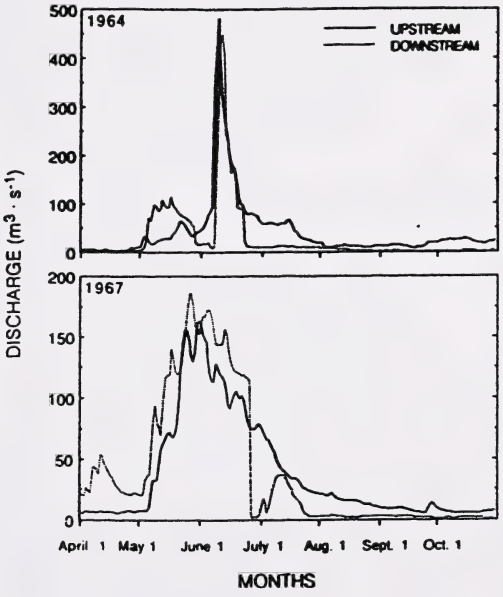
(reviewed in Rood and Mahoney 1990, 1993; Auble et al. 1994; Bradley and Smith 1986; Snyder and Miller 1991; Stromberg and Patten 1991, 1992). Regulation of the dam gates deliberately influences downstream flow patterns and can reduce or increase flows at specific times. The patterns of regulated flows downstream are dependent on the management objective for the dam, with two principal categories of patterns occurring for dams in the western prairies or Rocky Mountain foothills.

The first category of flow patterns typically involves flood-control or hydroelectric-generation dams. These dams are operated to attenuate seasonal flow patterns by trapping water during the high-flow periods and augmenting downstream flows during low-inflow periods. Downstream flow patterns are thus artificially stabilized.

The attenuation of flood flows will particularly impact seedling recruitment in downstream cottonwood forests (reviewed in Rood and Mahoney 1990, 1993; Scott et al. 1993; Stromberg et al. 1991). Flood flows are required for the dynamic stream erosion and deposition that underlies the active meandering of the stream channel and the creation of new, barren gravel, sand, and silt bars that are suitable for seedling establishment. In addition to the impact on the fluvial geomorphology, the high-flow period is essential to saturate the recruitment zones and subsequent gradually declining flows expose saturated recruitment sites and also provide moisture for the young seedlings. Attenuated flooding will thus reduce opportunities for cottonwood seedling recruitment.

Analyses of the historical flows of the lower St. Mary River demonstrate that flood flows are not dramatically altered. During the four decades following damming, major flood flows occurred in 1964 and 1975 and persisted downstream of the dam (Fig. 5). The timing of those flood flows may have been delayed by one or more days, and the specific pattern of the flood flows was slightly modified by the presence of the reservoir and by the artificial regulation of the dam's control gates. However, these changes were relatively minor and the magnitudes of major peak flows were generally similar upstream and downstream of the St. Mary Dam (Figs. 6 and 7).

Fig. 6. Hydrographs showing daily mean discharges for the St. Mary River upstream and downstream of the St. Mary River Dam for the period of April 1 to October 31 of 1964 and 1967, extremely high and very high (recurrence interval of 6.5 years) flow years, respectively.



Although the peak flows in flood years were relatively unaltered by the St. Mary Dam, the subsequent declining (falling limb) flows were often dramatically modified. Following the high-flow period in 1964, a relatively natural decline occurred until the flow dropped below about 100 $m^3 \cdot s^{-1}$ (Fig. 6). At that point, the control gates were closed and only a minimal flow was permitted downstream. Thus, the flood flow was followed by abrupt flow reduction and then a sustained period of minimal flow through the summer. This abrupt flow reduction would be accompanied by rapid water table decline that would be lethal for seedlings and might also be stressful for old cottonwoods (Mahoney and Rood 1991*a*, 1992; Segelquist et al. 1993). This pattern of abrupt flow reduction has been a common feature of river flow management along the St. Mary River following damming (Fig. 6).

In contrast to the flood year of 1964, the flow pattern of 1975 was relatively similar upstream and downstream from the St. Mary Dam (Fig. 7). Downstream flow reduction was slightly more rapid, but the alteration was less severe than in 1964, 1967, or other years with above-average peak flows. The flow pattern of 1975 may have been sufficient for initial seedling recruitment and would probably have been favorable to established trees. However, average and low flow years followed 1975, and the downstream flows during the summers of those years were minimal (Fig. 7). Successful recruitment and maintenance of established cottonwoods is a progressive response to long-term moisture patterns. Thus, although stream flows of 1975 would have been sufficient, flows in subsequent years would have been stressful.

Fig. 7. Hydrographs showing daily mean discharges for the St. Mary River upstream and downstream of the St. Mary River Dam for the period of April 1 to October 31 of 1975, an extremely high flow year, and the two following years.

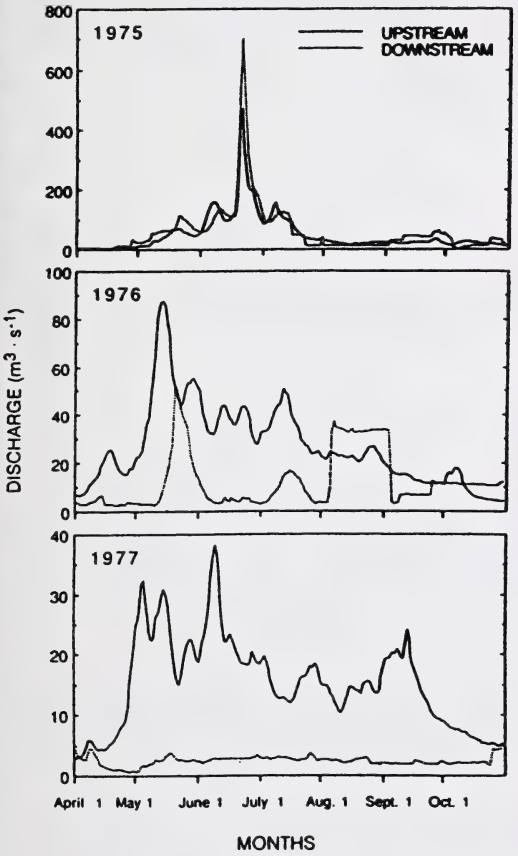
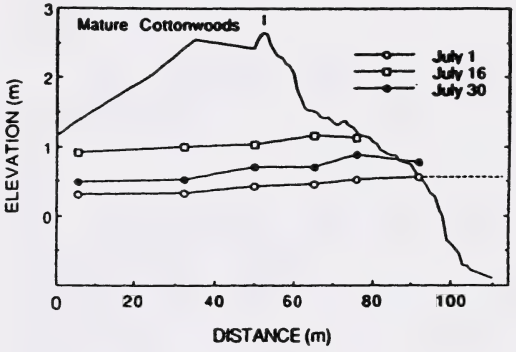


Fig. 8. Water table levels in six test wells positioned along a transect extending perpendicular to the St. Mary River at the Welling Ford, southern Alberta. Water table elevations are plotted for three dates in July 1993, and in each case the river stage was similar in elevation to the elevation in the well closest to the river edge. Elevations are scaled above a reference 0 m, which represents the river stage elevation at a flow of 6 $m^3 \cdot s^{-1}$, which would be a very low natural late summer flow. The broken line represents the river surface on July 1, 1993. Distance is from a reference balsam poplar tree that anchored the transect. Note that the elevation scale is greatly expanded relative to the distance scale.



Analyses of riparian water table levels

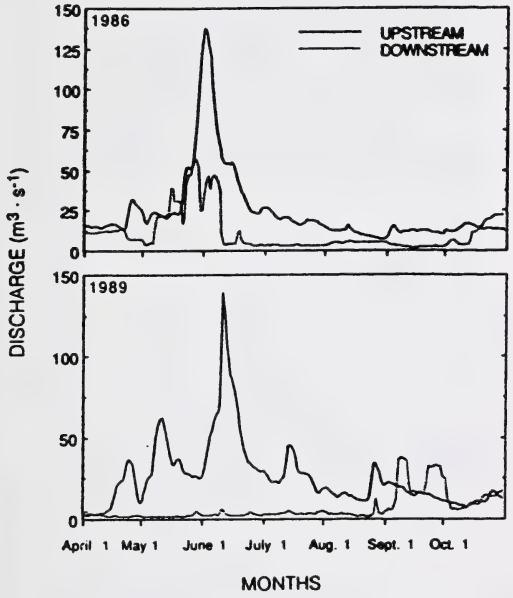
A close relationship between river stage (elevation) and water table depth is assumed for southwestern Alberta, since the riparian substrates consist largely of mixtures of sand, gravel, and cobble. Such mixtures would be relatively freely permeable (Mahoney and Rood 1992), enabling rapid water infiltration from or drainage to the river. High hydraulic conductivity is also indicated by observations of cutoff stream channels, abandoned gravel pits, and other ponds that continue to rise and fall in apparently close association with the rise and fall of the adjacent river.

The close linkage between river stage and riparian water table depth was confirmed in the present study through measurements of water levels in piezometers (test wells) positioned along transects in the riparian zone of the St. Mary River (Fig. 8). Water tables were measured weekly through the summer and generally demonstrated the pattern shown in Fig. 8, with a gradual decline in water table level extending away from the river's edge. For example, the water table sloped away at 31.5, 32.8, and 41.6 cm per 100 m on July 1, 16, and 30, respectively, and similar slopes were observed at most other dates. Exceptions consistently occurred immediately following changes in river stage when a lag in infiltration or drainage resulted in the water table sloping farther downwards or upwards, respectively, away from the river.

The piezometer study confirms that the riparian water table rises and falls in coordination with changes in the river stage and also indicates that the riparian water table is recharged by the river, providing an influent stream – water table situation. This situation would be consistent with the conclusion that these cottonwoods are reliant on water from the adjacent river (Busch et al. 1992) and also that reduced river flows downstream from the St. Mary Dam would create additional drought stress of the adjacent riparian cottonwoods.

These analyses reveal three features of the regulated flows along the lower St. Mary River. First, flood flows are relatively unaltered, and consequently a change to flooding patterns was not the cause of the decline of established trees or the failure of replenishment through new trees. Second, downstream flow reductions were frequently abrupt and these would probably be particularly stressful for cottonwoods (Mahoney and Rood 1991*a*, 1992). Third, prolonged periods of minimal flows occurred during the hot, dry periods of summer when evapotranspirational demand would have been highest. These minimal flows would have resulted in deeper riparian water tables, reducing water availability for the cottonwoods. Xylem water potentials of the three riparian cottonwood species in southern Alberta are naturally close to the threshold that results in xylem cavitation (Tyree et al. 1994). Further water stress imposed by insufficient stream flows would probably create further stress and possi-

Fig. 9. Hydrographs showing daily mean discharges for the St. Mary River upstream and downstream of the St. Mary River Dam for the period of April 1 to October 31 of fairly high flow years, 1986 (recurrence interval RI of 2.8 years) and 1989 (RI of 3.3 years).



bly catastrophic cavitation. The result would be branch and crown dieback and, eventually, complete shoot die-off, the patterns that were observed in field surveys downstream of the St. Mary Dam.

Over the four decades following the completion of the St. Mary Dam, there has been a continual expansion of irrigation agriculture in southern Alberta. Increases in irrigation acreage, expansion of canals to permit increased diversion flows and other changes have resulted in progressive increases in the amounts of water diverted from each of the rivers in the Oldman Basin. Consequently, although periods with high, average, or low stream flows have accompanied natural variations in regional precipitation (primarily variation in winter snow accumulation in the Rocky Mountain water sheds), the artificial hydrological impacts along the lower St. Mary River have generally increased over the past four decades. Thus, flows in the 1980s were particularly impacted, even during the higher inflow years of 1986 and 1989 (Fig. 9). The extensive commitment to irrigation in southern Alberta provides little opportunity for recovery of river flows along the lower St. Mary River which would be required for restoration of the riparian cottonwoods.

The present study confirms the previous observation of abrupt decline of riparian cottonwoods downstream from the St. Mary Dam (Rood and Heinze-Milne 1989) and demonstrates progressive loss over time. In contrast to the previous report, however, the present study indicates that cottonwood abundance downstream from the newer Waterton Dam has been relatively unchanged over the past three decades. The collapse of the cottonwood forests along the lower St. Mary River may be partly due to the more severe pattern of flow alteration and partly due to the natural suitability of the lower St. Mary River for riparian cottonwoods. In contrast to the lower Waterton River, cottonwoods were historically sparse along the lower St. Mary River, even prior to damming and water diversion for irrigation (Dawson 1885). The cottonwood abundance along the lower St. Mary River has consequently declined from sparse to almost absent.

It is likely that sparse cottonwood groves are particularly vulnerable to artificial impacts. The naturally sparse occurrence indicates that the local environment is only marginally suitable, and thus the existing trees would be functioning near the limit of their physiological range of adaptation. Consistent with this interpretation, there are almost no large, and consequently very old, cottonwoods along the lower St. Mary River. The lack of old trees also suggests that the environment is marginal, since (*i*) low-flow periods that would naturally occur at irregular intervals would lead to mortality preventing cottonwood survival for long periods, and (*ii*) old trees are probably particularly prone to stress-induced mortality (Albertson and Weaver 1945) and would thus be unable to survive marginal conditions. Following these lines of reasoning, the lower St. Mary River valley was apparently naturally only marginally suitable for cottonwoods, and consequently further stress imposed by artificial river flow reductions would be expected to have abrupt and severe impacts.

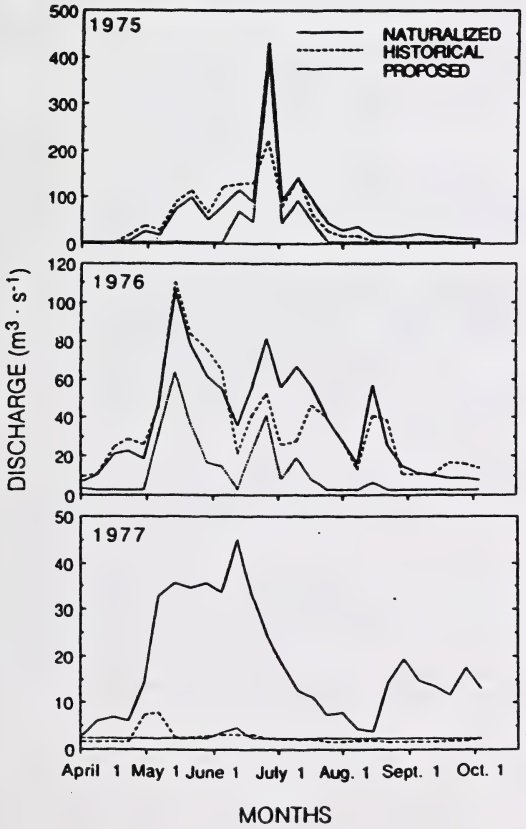
Future considerations

Subsequent to the previous report relating river damming and riparian cottonwood decline in southern Alberta (Rood and Heinze-Milne 1989), there have been a number of changes in the patterns of operation of the St. Mary and other dams in the Oldman River Basin. Allowable minimum flows were increased, in the case of the St. Mary River, from 0.93 to 2.75 $m^3 \cdot s^{-1}$. This increase will favor survival of established riparian vegetation but is probably still quite suboptimal for established trees and insufficient for seedling recruitment.

In recent years, the St. Mary Dam has been operated somewhat differently, allowing more gradual flow reductions following the high-flow period in late spring. The possible benefits of this operational adjustment are presently unclear, since the summers of 1992 and 1993 were exceptionally wet, confounding studies of the impacts from changes in dam operations. Providing some optimism, field surveys in 1992, 1993, and 1994 revealed additional saplings of narrowleaf cottonwoods and balsam poplars which probably resulted from clonal recruitment by root suckering. Clonal replenishment is common in southern Alberta (Rood et al. 1994) and may be particularly responsive to the recovery of stream flows, since root systems apparently remain viable even following severe shoot dieback (Stromberg and Patten 1989).

Although these recent changes provide encouragement for the preservation of some riparian cottonwoods in southern Alberta, the presently proposed operations plans for the rivers of the Oldman River Basin (Alberta Environment 1989*a*, 1989*b*) do not provide promise for recovery of the St. Mary cottonwoods (Mahoney and Rood 1993). There is little hope for substantial recovery of flows of the St. Mary River

Fig. 10. Hydrographs showing weekly mean discharges that would occur for the period of April 1 to Sept. 30 for the Waterton River for an extremely high flow year, 1975, and the two following years. Three lines are plotted, representing (*i*) naturalized flows, i.e., the estimated flows that would have occurred if no dams or water diversion existed; (*ii*) historical flows, i.e., the actual flows that did occur with the existing Waterton River Dam and actual historical levels of diversion in place at those times; and (*iii*) proposed flows, i.e., those that would be predicted to occur in a year with similar weather conditions to the years 1975 through 1977, but with the Oldman River Dam commissioned and consumptive uses increasing to the level approved by present provincial policies. Note that *y*-axis scales vary across the graphs.



in dry years when stream flows are low and irrigation demands are high. Without the commitment of increased flows during the dry periods it is unlikely that the cottonwood saplings that have emerged in the past 3 years will survive.

The presently proposed operations plan (Alberta Environment 1989*a*, 1989*b*) also raises concerns for the Waterton River cottonwoods. The present study suggests that those cottonwoods are still relatively abundant, although stressed. Proposed flow patterns for the lower Waterton River would become similar to the historical flow patterns of the lower St. Mary River (Fig. 10). Thus, there would be prolonged minimal flows during dry years, with stream inflows similar to those of 1977. Flows during average years similar to 1976 would be considerably reduced, and even in wet years with flows similar to 1975, flows would be reduced (Fig. 10). It is predicted that the combined impacts of these flow reductions would be accelerated mortality and reduced replenishment of the downstream riparian cottonwoods. It is consequently predicted that the forest groves would decline as the existing trees age and die.

In conclusion, the present study confirms the previous observation of abrupt decline of riparian cottonwood forests downstream from the St. Mary Dam. The observed 68% decline in the 35-year period between 1951 and 1985 is abrupt relative to the life-span of cottonwood trees and the decline was progressive over time. The decline is probably at least partly due to drought-induced mortality resulting from abrupt flow reductions and insufficient summer flows. Reduced river flows are accompanied by deeper riparian water tables, and this probably compounds natural drought stress leading to reduced xylem water potentials and consequent cavitation that underlies shoot dieback (Tyree et al. 1994). The current prognosis remains bleak for recovery of the cottonwoods along the lower St. Mary River, and proposed river management plans are also likely to impose further stresses on the cottonwoods along the neighboring Waterton River.

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River Damming and Riparian Cottonwoods Along the Marias River, Montana

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ABSTRACT: The Tiber Dam, completed on the Marias River, Montana, in 1956 moderates downstream flows by trapping spring flood flows and augmenting flows at other times, the total annual downstream flow is relatively unaltered. Cottonwoods, *Populus deltoides, P. balsamifera,* and *P. angustifolia,* and their interspecific hybrids occur along the Marias River and mature trees upstream and downstream from the Tiber Dam appear similar in health, with some branch and crown die-back. However, there is a severe deficiency of cottonwood seedlings downstream from the Tiber Dam.

The deficiency of cottonwood recruitment downstream from the Tiber Dam probably results from biological, hydrological and geomorphological consequences of stabilized river flows: (1) without exclusion due to flooding, zones of dense grass, shrubs, and sedges have encroached to the river's edge, competing with cottonwood seedlings, (2) the hydrological pattern of spring flooding and subsequent gradual flow decline required for seedling establishment is lacking, and (3) erosional and depositional processes are reduced, limiting the formation of point and lateral bars that are seedling recruitment sites. Additionally, (4) suspended silt settles out in the reservoir and consequently the downstream discharge carries little sediment that would contribute to bar expansion, and (5) the combined lack of flooding and impoverishment of suspended material may have resulted in an entrenched channel with steep stream banks, further degrading the cottonwood recruitment zone. With reduced seedling establishment, the downstream forests may be reliant on clonal regeneration that (1) is unlikely to be sufficient to compensate for ongoing mortality, (2) would probably disfavor *P. deltoides* since that species demonstrates little root suckering, and (3) would not introduce the genetic diversity that is essential for long-term forest adaptation. It is predicted that there will be a progressive decline of the riparian cottonwood forests downstream from the Tiber Dam unless a more dynamic river flow pattern is re-established.

KEY WORDS: cottonwoods, geomorphology, instream flow needs, *Populus*, riparian vegetation, river damming, seedlings

INTRODUCTION

The semi-arid areas of North America's western prairies and Rocky Mountain foothills are characterized by a general lack of large, woody vegetation. In contrast to the prairie uplands, the river valleys receive additional water from the streams enabling the development of riparian woodlands that consist primarily of cottonwood (poplar) trees, willows and shrubs. These riparian forests provide aesthetic, recreational, and environmental relief in the otherwise treeless regions and generally provide the richest wildlife habitats in these areas (Finch and Ruggiero 1993).

Over the past century, riparian cottonwood forests have declined sharply across southwestern North America (Johnson and Jones 1977; Rood and Mahoney 1990). Causes for the decline include clearing for pastures and crop production, harvesting for fuel and building materials, livestock grazing, and various other human impacts. Additionally, river damming has resulted in the downstream decline of cottonwoods along many rivers in the western prairies and Rocky Mountain foothills (reviewed in: Rood and Mahoney 1990). The influences of river damming and water diversion can be severe and widespread along river valleys since impacts can extend downstream at least as far as the flow pattern is altered, distances of up to hundreds of kilometers (Williams and Wolman 1984). The negative impacts of river damming result from a number of changes downstream and the specific causes of riparian forest decline vary across rivers (Rood and Mahoney 1990). However, two general patterns of negative impacts emerge.

Firstly, some damming projects create drought stress on downstream forests due to the diversion of water offstream, primarily for irrigation (Johnson and Jones 1977; Rood and Heinze-Milne 1989; Rood and Mahoney 1990; Snyder and Miller 1991; Stromberg and Patten 1992). Secondly, some dams are operated to change the downstream flow pattern, particularly to attenuate spring flooding and provide annual flow stabilization. Cottonwood replenishment is dependent on dynamic hydrological and geomorphological patterns and consequently, flow stabilization reduces cottonwood seedling replenishment (Bradley and Smith 1986; Fenner et al. 1985; Rood

and Mahoney 1990; Scott et al. 1995; Stromberg et al. 1991).

To understand the causes of riparian cottonwood forest decline and to enable the development of dam operation plans that will sustain and even enhance riparian forest replenishment, numerous dammed and undammed river systems must be analyzed. By integrating analyses from various rivers, it should be possible to determine general relationships between instream flows, channel processes and riparian cottonwood recruitment and survival.

Historical Background - The Marias River

The Marias River originates at the confluence of Two Medicine River and Cutbank Creek, streams that drain relatively pristine headwaters in Glacier National Park, Montana (Figure 1). These streams flow through the relatively undeveloped Blackfoot Indian Reservation, and then flow east and south through sparsely populated agricultural lands, before joining the Missouri River.

(Figure 1 near here)

The Tiber Dam was completed on the Marias River in 1956, about two-thirds of the distance from the headwaters to the river's outflow. The 63 m high zoned, earth-fill dam creates 'Lake' Elwell that has a total storage capacity of 1.68 million dam^3, about three times the river's average annual flow (USDI/BR 1983). This proportionally large storage capacity enables substantial flood flow attenuation.

Originally planned to provide irrigation water, only about 1200 ha were irrigated from the reservoir in 1992 although the system has an adequate capacity to allow the irrigation of more than 51,000 ha (USDI/BR 1983). While the irrigation function has not been utilized extensively, the reservoir and dam have contributed to flood control of the Missouri River system and the top 5.9 m of water storage (about 492,000 dam^3) is allocated for flood control.

The Marias River is adjacent to the St. Mary (Rood and Heinze-Milne 1989; Rood et al. 1995), Milk (Bradley and Smith 1984; 1986) and Missouri rivers (Hansen 1989; Johnson 1992; Scott et al. 1995), other dammed rivers along which the impacts of river damming on riparian cottonwoods have been studied. These rivers have some shared and some distinctive hydrological and ecological characteristics. The present study investigated the direct and indirect impacts of river damming and flow regulation that influence riparian cottonwood forests along the Marias River. Conclusions from this study complement previous analyses of the adjacent and distant dammed rivers.

MATERIALS AND METHODS

Field studies were conducted on the Marias River in the summers from 1990 through 1994. The field data and photographs presented in this report were collected on August 2 and 3, 1990, June 25 to 28, 1991, August 14, 1992, May 27, 1993, and July 10 to 12, 1994. The data and discussions presented in this paper are considered to be representative of conditions observed during other site visits that were also conducted.

River stage/discharge ratings data and historical river discharge data were provided by Mr. Ron Shields, United States Geological Survey, Montana and Mr. Tim Personius, United States Department of the Interior, Bureau of Reclamation, Montana. Information regarding the development and management of the Tiber Dam and Elwell reservoir and the management of the Marias River Basin were provided by Mr. Tim Personius, Mr. Buck Damone, Bureau of Land Management (BLM), Lewistone, Mr. Jim Wedeward, BLM, Billings and Mr. Stan Huhtala, at the Tiber Dam (and USDI/BR 1983).

Mean daily, monthly, and annual discharge data for the Marias River downstream of the Tiber Dam were obtained for the years 1946 and 1947, prior to the construction of the Tiber Dam, and continuously from 1956 to 1994 (gauge south of Chester, hydrometric station 06101500). Data were obtained for the upstream reach for the intervals from 1902 to 1908 and from 1911 to 1994 (gauge south of Shelby, station 06099500).

Upstream versus downstream comparisons investigated vegetation and stream bank elevations relative to river stages. Due to the flow modifications from the Tiber Dam, discharges varied for the upstream versus downstream reaches, complicating direct comparisons. To compensate for the flow differences, daily mean discharges and discharge/stage ratings curves were used to determine relative elevations above a reference stream stage at 8.5 m^3/s (300 ft^3/s). This value was determined from annual hydrographs for the unregulated upstream reach, as being typical of the late season flow (Oct. and Nov.). The estimated river stage at 8.5 m^3/s was established as '0' and vegetation and stream bank elevations are expressed relative to this base reference.

Elevation calculations for all of the upstream sites were based on the stage/discharge

ratings function for the upstream hydrometric gauging station while calculations for the downstream sites were based on the ratings curve for the downstream station. It should be recognized that these ratings curves were not specific to the individual field sites and consequently the elevation determinations are estimates.

Floodplain distances (from the river) are based on a reference point corresponding to the estimated position of the river edge at a river stage 60 cm above that of the reference '0' stage at 8.5 m^3/s. This stream bank reference position was ecophysiologically based as the typical lower limit of the successful cottonwood seedling recruitment zone (Bradley and Smith 1986; McBride and Strahan 1984; Noble 1979; Stromberg et al. 1991). The establishment of this reference position enables comparison of upstream versus downstream conditions relative to the suitability for cottonwood seedling recruitment. The assignment of this reference stream bank position did produce a few negative values since some sampling occurred when the river stage was less than 60 cm above the 8.5 m^3/s stage.

Site locations and feature names are based on 1:24,000 U.S. Geological Survey maps that were plotted from 1965 air photos, field checked in 1967 (upstream), or 1969 air photos, field checked in 1970 (downstream). During site visits, observations regarding cottonwood forest condition and the extent of branch and crown die-back were noted and photographs were taken at four access points upstream (Highway 15, Williamson Park, Naismith Siding, and F Bridge) and downstream (Sanford Park (Tiber Dam), Pugsley, Moffat and Circle (Highway #223) bridges) of the Elwell reservoir. Surveys of the continuous reaches were conducted by canoe trips between June 25 and 28, 1991 from Naismith Siding to the F Bridge (upstream) and from Sanford Park to the Circle Bridge (downstream). Canoe trips from July 10 through 12, 1994 included the same reaches and also a trip from the Shelby Golf Course to Williamson Park. During river trips, observations regarding cottonwood occurrence and condition were recorded and stops were made at each major meander lobe.

At meander lobes selected for sampling, transects were established perpendicular from the river's edge up the stream bank for a distance of 100 m or until the elevation reached 2 m above the river stage. Transects were surveyed for elevation, and surface

composition and vegetation zones were mapped and described. The occurrences of cottonwoods within 1 m on either side of the transects were noted, tree diameters at a height of about 1.2 m were measured and tree heights were estimated by triangulation. Percent vegetation cover was estimated using a 1 m^2 quadrat containing a twenty junction string grid; the number of junctions falling on vegetation versus barren surfaces were counted. Seeds and seedlings were counted in a 0.65 m^2 quadrat positioned at intervals along the transect within 10 m of the stream edge. Tree condition and the extent of branch and crown die-back were rated on a 5 point scale (1 - standing dead to 5 - very healthy, no dead branches). Typical cottonwood leaves were collected and taxonomic status was assigned based on leaf morphology (Eckenwalder 1984; Rood et al. 1986).

While the study focussed on the river reaches within 30 river km upstream and downstream of Lake Elwell, other sites along the lower Marias River to the junction with the Teton (Montana) and Missouri rivers and upstream through the foothills region and into Glacier National Park to the Marias Pass were also visited. To assess an adjacent, undammed river, the Teton River was visited with particular attention to the downstream reach that joins the Marias River near the Missouri River. Cottonwood leaves were collected, the general occurrence and health of cottonwoods were noted, and the stream banks were studied with respect to the vegetation cover adjacent to the river. The occurrence of barren lateral and point bars that would be suitable for cottonwood seedling establishment, the sizes of cottonwoods present and the abundance and distribution of seedlings and saplings were also noted and photographed.

RESULTS AND DISCUSSION

Stream Flows Upstream and Downstream from the Tiber Dam

The two gauging stations on the Marias River are ideally situated upstream and downstream from Lake Elwell (Figure 1). Between these gauging stations, Pondera Creek from the south, Willow Creek from the north, and other smaller creeks flow into the Marias River and Lake Elwell. However, these small creeks primarily drain prairie areas and provide only minor contributions to the Marias River discharge. Consequently, river discharges at the two gauging stations were very similar prior to the installation of the Tiber Dam (Figure 2). This pre-damming comparison indicates that this river reach is in hydrological equilibrium, with losses due to infiltration into the adjacent riparian water table and evaporation being balanced by ground water and tributary inflows. Differences between the upstream and downstream flows after 1956 can therefore be attributed almost entirely to the operation of the Tiber Dam.

(Figure 2 near here)

Operation of the Tiber Dam has had little impact on the total annual downstream discharge of the Marias River (Figure 3). With the exception of 1956, the year during which the reservoir was filled, upstream and downstream annual discharges were very similar (Figure 3). Thus, the Tiber Dam has not been operated to store water in the Elwell reservoir from one year to the next.

(Figure 3 near here)

The period of hydrologic record includes the major flood years of 1964 and 1975 (Figures 3 and 4) and some naturally low flow years, including 1973, 1977 and 1988 (Figure 3). 1988 is noteworthy because the summer was very dry and substantial

premature leaf senescence, and subsequent branch and crown die-back were observed for cottonwoods along the adjacent St. Mary River and other dammed rivers in the Oldman River Basin.

(Figure 4 near here)

The post-damming period thus included high and low flow years that would naturally contribute to riparian cottonwood recruitment and to mortality. For example, the variation in mean discharge between 1975 and 1977 was 6.3 fold (upstream, 1975 flow/1977 flow; Figure 3). It is probable that such natural variation in annual river discharge and particularly, periods of multiple high or low flow years result in the naturally irregular population cycling of riparian forests, with episodes of increased forest recruitment and intervals of forest decline (Baker 1990). For example, the natural drought of the 1930's induced widespread riparian cottonwood mortality across the western prairies (Albertson and Weaver 1945). The fluctuation in total annual discharge was maintained downstream from the Tiber Dam (1975 flow/1977 flow = 6.4) and thus, this dynamic component of the river flow pattern has not been altered by the Tiber Dam (Figure 3).

Although total annual flows were unchanged, the seasonal flow pattern has been dramatically altered (Figure 5). The annual high flows that naturally occurred during May and June were consistently reduced downstream due to partial peak trapping by the reservoir. Subsequently, during the naturally lower flow periods of July through November, downstream flows were augmented as the trapped spring snow melt was gradually released (Figure 5).

(Figure 5 near here)

This seasonal flow moderation involves flood flow attenuation, which is a prime management objective for the Tiber Dam. After damming, two major flood years

occurred, 1964 and 1975 (Figure 4 and 6). Due to flow attenuation, downstream peak flows during these years were in the order of one-tenth of the upstream peaks (Figure 4). The peak flows in 1964 and 1975 were thus reduced from flood events with one in ninety and one in forty-five year recurrence intervals, respectively, to flows corresponding to a natural (upstream) return interval of about one in five years (Figure 4). The post-peak flow patterns were also dramatically altered downstream from the Tiber Dam throughout the summers of 1964, 1975 and other high flow years (Figure 6).

(Figure 6 near here)

Riparian Cottonwood Species

Similar to the situation in the Oldman River Basin (Brayshaw 1965; Rood et al. 1986; Greenaway et al. 1989), three cottonwood species occur along the Marias River: the prairie cottonwood, *Populus deltoides*, the balsam poplar, *P. balsamifera* and the narrowleaf cottonwood, *P. angustifolia* (Fig. 7). Leaf forms intermediate between the species commonly occurred, indicating the presence of interspecific hybrids. Consistent with the situation along the nearby Oldman and St. Mary rivers (Rood et al. 1986), balsam poplars were prevalent along the Marias River near the Rocky Mountains whereas prairie cottonwoods were more abundant downstream near the junction with the Missouri River. All three species occurred at intermediate elevations and trispecific occurrence and hybridization was prominent along the upstream and downstream study reaches (Figure 1).

(Figure 7 near here)

There are certain to be various ecophysiological differences across the cottonwood species. The narrowleaf cottonwood grows more slowly than the other species (Campbell et al. 1993) while the prairie cottonwood may be more vulnerable to

drought-induced cavitation (Tyree et al. 1994). We did not systematically investigate differences across the cottonwood species present and future investigations could study species-specific patterns of seedling recruitment and mortality.

Impacts of Stream Flow Regulation on Established Cottonwoods

The hydrographs presented in Figure 5 represent patterns averaged over more than three decades. As shown for high flow years (Figure 6), the annual downstream flow patterns deviate even further from the natural patterns than does the overall mean. For example, during the 1980's, maximal monthly flows downstream of the Tiber Dam occurred in July (1980), August (1984), September (1987), October (1986), November (1985) and even January (1988), while the natural peaks upstream consistently occurred in May or June.

It is physiologically appropriate that cottonwoods have evolved to grow branches during May and June (J. Willms and S.B. Rood, unpublished). This is the natural period of high stream flow and consequently, adequate moisture is available to maintain turgor pressure that underlies cell enlargement and maintains open stomata, permitting gas exchange and subsequent photosynthesis. The artificially altered seasonality of river flow would probably be unfavorable for the May and June growth of established riparian cottonwoods along the lower Marias River. In particular, the reduction of flows in the late spring would reduce the growth and health of riparian cottonwoods located furthest away from the stream's edge, and at the highest elevations above the stream. The reduction in late spring recharge of the riparian water table is thus one probable negative impact of stream flow alteration along the lower Marias River.

Countering the negative impact of reduced flows in May and June, augmented stream flows in July and August (Figure 5 and 6) have probably been favorable for established cottonwoods. Although branch growth is probably complete by mid-July, leaves remain on the trees and gas exchange continues throughout the summer (Tyree

et al. 1994). This may enable continued radial growth and leaf production. It may also be important for tree survival through the winter and for the production of carbohydrate to fuel the resumption of physiological activity the following spring. The hottest periods with the highest evapotranspirational demands generally occur in July and August and augmented flows during this period would reduce drought stress and consequently be favorable for riparian vegetation.

Flow augmentation after the summer and following leaf senescence and abscission is less likely to benefit cottonwoods. Flow augmentation through the late autumn and winter would thus have less benefit for riparian vegetation than increased stream flow during the physiologically active period from May through September.

With respect to the overall growth of established cottonwoods, stream flow reduction during May and June is probably slightly unfavorable whereas flow augmentation during July and August is probably beneficial. These two alterations are likely to counter one-another to produce relatively little net impact on the established cottonwoods along the lower Marias River. Consistent with this conclusion, established cottonwood forests downstream and upstream from the Elwell reservoir appeared generally similar in health with most stands receiving average ratings of about 4 (a few dead branches) with respect to general appearance of health. Some evidence of branch and crown die-back was observed, but this is a natural component of riparian cottonwood forests, and probably represents the mortality of individual branches due to xylem cavitation during the hot, dry periods in mid-summer (Tyree et al. 1994).

The continuing health of established cottonwoods downstream from the Tiber Dam contrasts with the abrupt decline of cottonwoods that occurred after damming along the adjacent lower St. Mary River (Rood and Heinze-Milne 1989; Rood et al. 1995). The Tiber Dam on the Marias (1956) and the St. Mary Dam (1951) were installed at about the same time and the downstream cottonwood stands involve the same species and hybrids.. The regions share generally similar climatic conditions and both rivers drain the eastern areas of Glacier National Park. Thus, the watersheds and upstream inflow

patterns are similar. However, the dams are operated for different purposes and downstream flows differ dramatically. Spring flooding persists downstream of the St. Mary Dam but summer flows are severely reduced as water is diverted offstream at the reservoir for irrigation (Rood and Heinze-Milne 1989; Rood et al. 1995). In contrast, flood flows are trapped by the Tiber Dam and downstream flows are augmented in the summer (Figures 3, 5 and 6). The different impacts on the cottonwoods along these two adjacent dammed rivers indicates that it is the pattern of flow regulation and not simply the presence of dams that determines the fate of the riparian cottonwoods downstream. This conclusion is consistent with the observed diversity of cottonwood responses downstream from other dams (Rood and Mahoney 1990) and there are cases in which cottonwood forests have increased following damming and river flow regulation (Johnson 1994).

A further conclusion can also be reached following the comparison of the lower Marias and St. Mary rivers. Adequate summer stream flow is essential for the sustenance of established riparian cottonwoods. This conclusion is physiologically sound and supports the need for the development of instream flow recommendations that include sufficient summer flows (Stromberg and Patten 1990).

Influence of Altered Stream Flows on Cottonwood Seedling Recruitment

While the previously established cottonwoods have not been seriously affected by river damming and flow regulation along the Marias River, the recruitment of cottonwood seedlings has been severely reduced. Seedlings were abundant on all meander lobes along the upstream reach but were scarce downstream of the Tiber Dam (Figure 8). Seedling densities in the recruitment zones of the nine upstream and nine downstream transects averaged 114 (s.d. 151.8) and 2.6 seedlings/m^2 (s.d. 3.1), respectively, for the studies in 1991 and 1993 (unpaired t-test, t value 2.217, P=0.04). This represented a forty-fold difference and every upstream transect contained more

seedlings than any downstream transect. Even these values probably underestimate the severity of the decline of seedlings. In 1994, studies were modified to search specifically for arcuate bands of cottonwood seedlings that occur along river meanders at specific elevations that had satisfactory moisture and substrate conditions and received abundant seeds by wind and water (river) deposition. Arcuate bands with up to 500 one to three year old seedlings per m^2 were abundant along the upstream reach but no such bands were observed downstream from the dam.

Numerous wind-borne and floating cottonwood seeds were observed at all sites both upstream and downstream of the Elwell reservoir and abundant seedlings were observed on artificially barren sites adjacent to Sanford Park, shortly downstream from the Tiber Dam. Thus, the deficiency of cottonwood seedlings downstream from the Tiber Dam is neither due to a shortage of seed, nor to poor seed viability. Instead, it is due to the scarcity of suitable seedling recruitment sites and lack of the required hydrological pattern.

(Figure 8 near here)

The severe deficiency of seedling recruitment downstream from the Tiber Dam was very probably due to direct and indirect, biological, hydrological and geomorphological consequences of flood flow attenuation. The following sections describe these impacts and are presented in descending order of proposed importance relative to the scarcity of seedling replenishment. Of these impacts, the first discussed, the encroachment of stream bank vegetation, probably provides the most obvious difference between the riparian zones along the upstream versus downstream reaches (Figure 8).

1. Encroachment of Stream Bank Vegetation. Riparian cottonwoods and willows are more flood tolerant than most neighboring plant species and particularly those species that normally occupy higher and drier zones away from a stream (Hosner, 1958). Annual flooding excludes the flood intolerant species from the lower elevations of the

stream banks, areas that provide the principal recruitment zones for cottonwood seedlings. Cottonwood seeds and seedlings are extremely small (Bessy, 1904) and with correspondingly limited cotyledonary fuel reserves, cottonwood seedlings are not competitive against established vegetation. Thus, cottonwood and willow seedling recruitment is reduced by vegetation cover (Stromberg et al. 1991).

In contrast to the natural situation along the upstream reach, the attenuation of flooding downstream of the Tiber Dam has resulted in the failure to exclude flood intolerant species from the areas adjacent to the stream. Consequently, a zone of dense vegetation has encroached right to the river's edge (Figures 8 and 9). The streamside zone was dominated by various grasses and some sedges (*Carex* sp.). With rising stream bank elevation, shrubs became more abundant, including *Symphocarpus occidentalis* (western snowberry or buckbrush), *Rosa woodsii* (wild or woods rose), *Prunus virginiana* (chokecherry), and *Shepardia argentea* (thorny buffalo-berry). Various forbs also occurred, including *Cirsium arvense* (Canada thistle).

(Figure 9 near here)

Although very few cottonwood seedlings occurred, and cottonwood saplings (with stem diameters less than 10 cm) were sparse in the riparian zones downstream from the Tiber Dam, riparian willows (*Salix exigua* (sandbar willow) and some *S. amygdaloides* (peach-leaf willow)) were generally still abundant. This indicates that the impacts of stream flow regulation vary across riparian species, especially between cottonwoods and willows. This difference may be due to underlying differences in the reproductive process. Cottonwoods are more reliant on seedling replenishment whereas willows are apparently better able to reproduce through the clonal processes of shoot and root suckering.

While increased vegetation cover in the riparian zone has had the unfavorable consequence of preventing cottonwood seedling recruitment, it has had another impact

that would generally be considered favorable. The proliferation of exotic species in riparian areas is a problem across western North America. The naturally dynamic riparian processes invoke frequent disturbance and the creation and/or exposure of barren areas that are vulnerable to immigration of aggressive exotics. In northcentral Montana the most abundant invader is generally leafy spurge (*Euphorbia esula*), a durable plant with a range of reproductive strategies that produces various phytochemicals that retard wildlife or cattle forage and may inhibit the germination and growth of adjacent plants (Best et al. 1980).

Leafy spurge was very abundant along the upstream reaches of the Marias River and has become the most abundant plant in the riparian zone in some areas. In contrast, leafy spurge occurred only sparsely along the downstream reach. The reduced abundance of leafy spurge was probably due to the existence of established vegetation and subsequent lack of barren areas accessible for invasion. This same pattern of decreased abundance of an aggressive exotic downstream had apparently also occurred for sweet clover (white, *Melilotus alba* and especially yellow, *Melilotus officinalis*).

2. *Lack of Essential Pattern of Stream Stage Change.* With respect to direct hydrological impacts, there are specific, dynamic stream stage patterns that are essential for successful seedling replenishment of cottonwoods (Bradley and Smith 1986; Mahoney and Rood 1993; Rood and Mahoney 1990; Scott et al. 1995). High stream stages are required in late spring to saturate seedling recruitment sites. The high flow period must occur prior to or during the period of seed dispersal, a period that extends from early or mid-June through July along the Marias River. The stream flows must then decline to expose the saturated and barren recruitment sites upon which cottonwood seeds land following wind or water dispersal (Bradley and Smith 1986; Mahoney and Rood 1993). If suitable moist sites exist, seed imbibition and germination are rapid. Cottonwood seed viability is almost complete initially, but falls abruptly within a few weeks (Moss 1938).

Initial seedling establishment is not generally the limitation to cottonwood

recruitment, but instead seedling survival is the component of the life cycle that generally limits the cottonwood population. Seedling mortality is very high, and is primarily drought-induced (Moss 1938). For seedling survival, stream stage decline must be sufficiently gradual that root growth of the small and vulnerable seedlings is able to maintain functional contact with the capillary fringe that exists above the declining riparian water table (Figure 8) (Mahoney and Rood 1991; McBride et al. 1988; Segelquist et al. 1993). Except following abrupt stream flow changes, the water table represents a relatively horizontal extension from the stream stage (Rood et al. 1995) and consequently, the rate of riparian water table decline closely follows the rate of river stage decline. Thus, for cottonwood seedling survival, the rate of river stage decline must not greatly exceed the rate of cottonwood root elongation growth.

The specific pattern of stream stage change that is required for cottonwood seedling recruitment including: (1) high late spring stage, (2) initial rapid stage decline and then (3) gradual stage decline, naturally occurs at irregular intervals of about one in two to one in ten years, during, or possibly following, years with moderate major peak flows (Baker 1990; Bradley and Smith 1986; Scott et al. 1995; Stromberg et al. 1991). The artificial stream pattern along the lower Marias River over the past three decades has not provided this essential stage change pattern during high or moderate flow years (Figure 6). Consequently, the artificial alteration to the spring and summer stream flow pattern presents a direct hydrological impediment to the seedling recruitment of cottonwoods.

3. *Geomorphological Change due to Attenuated Flooding.* While the alteration to stream flow pattern will directly influence cottonwood seedling establishment, there will also be indirect influences due to geomorphological changes (Williams and Wolman 1984). Flood flows in the late spring produce the highest river stages and the highest stream velocities. These combine to produce physical conditions most competent to move materials in the stream channel and banks. Thus, high stream flows drive river meandering and the production of point bars along meander lobes.

These gradually sloping, newly deposited point bars are barren and saturated and provide the principal sites for the successful establishment of cottonwood seedlings (Figure 8). As with adjacent flood-flow attenuated rivers (Bradley and Smith 1984; Johnson 1992), the moderation of high flows along the Marias River would prevent the dynamic meandering and the production of new barren point and lateral bars. This geomorphological change results in the lack of seedling recruitment sites and thus, provides an indirect negative impact on cottonwood seedling replenishment (Johnson 1992).

Although further studies of channel geomorphology of the Marias River would be useful, it is probable that the patterns observed downstream from the adjacent Fresno Dam on the Milk River are likely to be similarly occurring on the Marias. As described by Bradley and Smith (1986), downstream from the Fresno Dam, another flood control dam, channel width was reduced, the rate of meander migration was substantially reduced, and channel bed degradation occurred, particularly near the dam.

4. Impoverishment of Suspended Sediment Loads - the Silt Shadow. As with virtually all dams (Williams and Wolman 1984), a silt shadow exists downstream from the Elwell reservoir; there is a scarcity of suspended material in the water outflowing from the Tiber Dam (Figure 10). Recovery of the suspended sediment load was gradual and remained low over the 30 km downstream reach (Figure 10). High water clarity downstream from the Tiber Dam is typical year-round and this probably favors the prosperous cold-water sport fishery that occurs downstream from the dam (S. Hutla, personal communication).

(Figure 10 near here)

The development of recruitment sites is dependent on the dynamic hydrological pattern described previously (2 above), on the dynamic meandering that enables the

creation of point and point bars (3) and, for some cottonwood species, on the the deposition of sand and silt on those bars. Consistent with the case along the Missouri River (Johnson 1992), the impoverished suspended sediment load due to the silt shadow further prevents the development of seedling recruitment sites along the downstream reaches of the Marias River.

5. Stream Bank Configuration. Due to the silt shadow, channel degradation occurs downstream from most dams (Williams and Wolman 1984). This has probably occurred downstream from the Tiber Dam and as a result, some entrenchment may have followed, altering the elevation profile of the stream banks (Figure 11). On meander lobes of the free-flowing upstream reach, the stream bank consistently rose gradually away with a typical slope of about 5 cm/m (Figure 11). This gradually sloping bank provides a large area within the elevation range that defines the successful cottonwood recruitment zone, a zone that is typically about 60 to 150 cm above the late summer river stage. In contrast to the upstream condition, the stream bank downstream sometimes involved a steeper step through the cottonwood recruitment zone (Figure 11). This would further reduce the opportunity for cottonwood seedling establishment on the downstream reach.

(Figure 11 near here)

6. Vegetative Armoring of the Stream Banks. Dynamic processes in the riparian zone involve the interactions of hydrology, geomorphology and vegetation. Vegetation influences the physical system, affecting both the hydrology and geomorphology. Along the lower Marias River, the dense zone of sedges, grasses and shrubs reduces the erosion of the stream banks (Figure 8). The dense vegetation band has provided a vegetative armoring that has probably retarded stream bank degradation and channel meandering. The dynamic nature of the lower Marias River is already reduced due to the lack of flooding. Vegetative stream bank armoring would further stabilize the

channel configuration. Recognizing that the seedling replenishment of riparian cottonwoods is dependent on a dynamic stream channel, vegetative armoring probably compounds the geomorphological problems and further hinders the recruitment of riparian forests.

Quantitative Considerations

Most of the patterns described above were observed at all sites during the present study. Thus, at all nine upstream transects, relatively barren zones existed on the meander lobes and these supported abundant cottonwood seedlings (impacts #1 and #3). Conversely, at all nine downstream transects, dense vegetation extended right the river's edge and no barren zones occurred. These patterns were also consistent across the five years of the study.

As demonstrated by the hydrological analyses, similar consistency would occur for all components directly driven by stream discharge. No flood events have occurred downstream from the Tiber Dam and thus, all geomorphological events driven by flooding would have been prevented (impact #3) (Figures 4 and 6).

The present study was not intended to provide a comprehensive analyses of geomorphological impacts but many could be predicted with reasonable confidence based on studies of adjacent and distant dammed streams (Bradley and Smith 1984; Johnson 1992; Williams and Wolman 1984). Similarly, the impoverishment of suspended sediment downstream from the Tiber Dam could be confidently predicted and was also consistently observed at downstream sites during the present study (impact #4) (Figure 10).

Only one pattern described above was apparently variable in the present study. A change in stream bank configuration (impact #5) (Figure 11) was suggested by elevational profiles at some, but not all, downstream transects. Of the nine transects, two had abrupt elevation steps, four produced intermediate steps similar to the downstream profiles presented in Figure 11 and three included gradually

sloping banks that were similar to those of the upstream meander lobes. Due to this variation, the comparison of nine downstream and upstream transects was insufficient for confident conclusions regarding changes in stream bank configuration. Even with the survey of additional transects, statistical comparison of elevation profiles would be confounded because the base elevation estimations were based on common discharge/stage functions. If the stream channel configuration has been altered, then the discharge/stage functions would be correspondingly altered. Thus, further investigation of this possible impact must include transect-specific discharge/stage determinations.

The results of the present study alone are insufficient to establish a correlation between river damming and downstream impacts on riparian cottonwoods. However, the impacts observed were consistent with reported impacts along other adjacent and distant dammed streams. The present study thus supports other studies that indicate that river damming can result in the decline of downstream cottonwood forests. An important contribution from the present study is that the encroachment of stream bank vegetation (#1) may be another major consequence of stream flow regulation that would hinder cottonwood recruitment. That this impact has not been previously emphasized is somewhat surprising since it was particularly prominent in the present study and this impact alone would severely retard opportunities for seedling replenishment.

Future Prospects for Riparian Cottonwoods Along the Lower Marias River

The preceding analyses of river flow and riparian vegetation and preliminary assessments of geomorphology consistently indicate that cottonwood seedling recruitment is failing downstream from the Tiber Dam. It is probable that if the operation of the Tiber Dam continues in the pattern of the past four decades, the deficiency of seedling recruitment will continue. Subsequently, it is likely that as the previously established trees age and die, the riparian forests will progressively decline due to insufficient replenishment. This would result in a gradual loss of riparian cottonwoods over the next half-century downstream of the Tiber Dam.

There are biological components that could provide some resiliency for the Marias River woodlands. These forests include the trispecific hybrid swarm of prairie cottonwood and the two closely related species, the balsam poplar, and the narrowleaf cottonwood. While seedling establishment provides a prominent method of recruitment of new trees, the balsam poplar and narrowleaf cottonwood are also capable of prolific root suckering, the production of adventitious shoots from existing roots (Rood et al. 1994). Root suckering enables clonal propagation, broadening the trees' potential for expansion. Suckering is probably induced or promoted by different environmental conditions than those needed for seedling establishment and may be particularly important for cottonwood stands associated with severely altered stream flow regimes (Stromberg et al. 1989). Other forms of clonal regeneration exist for all three species, including shoot suckering (coppicing), shoot regrowth after burial or decapitation due to ice shearing, beaver browsing or fire (Rood et al. 1994). Coppice regrowth was observed along the Marias, both upstream and downstream from the Tiber Dam, although quantitative patterns were not investigated.

Asexual reproduction, particularly through root suckering, might enable some cottonwood propagation even though seedling establishment is deficient along the lower Marias River. The prospects for long-term sustenance of the cottonwood forests

through suckering is uncertain although clonal recruitment could slow the cottonwood decline that would follow the failure of seedling replenishment. A similar situation may exist along the Bow River, downstream from Calgary, Alberta, where a sequence of hydroelectric dams result in flow attenuation, somewhat similar to that occurring along the Marias River. Along the lower Bow River, it is likely that seedling recruitment is deficient, but some saplings still exist and many of these probably result from suckering of balsam poplars (Rood and Bradley 1993). Unlike the Bow River, however, along the Marias River, there would probably be changes in forest composition with continued reliance on clonal recruitment. Since prairie cottonwoods root sucker very rarely (Rood et al. 1994), it is likely that this species will become proportionally reduced over time, while the balsam poplars and narrowleaf cottonwoods that are better able to reproduce clonally will proportionally increase.

In conclusion, seedling recruitment of cottonwoods is failing along the Marias River, downstream of the Tiber Dam. The failure is probably due to the direct and indirect biological, hydrological and geomorphological consequences of damming and particularly, flood flow attenuation. Due to this failure, a gradual decline in forest abundance is expected as seedling recruitment fails to replace established trees as they age and die. Some compensation for the lack of seedling reproduction may occur through clonal propagation, although that will lead to reduced forest biodiversity and a failure to introduce the genetic variability that is essential for long-term adaptation. Recovery of the natural reproductive cycling of riparian forests along the lower Marias River will require the reestablishment of more dynamic stream flow patterns, including the recovery of some degree of flooding.

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Figure Captions

FIGURE 1. Map of north central Montana showing the location of the Marias and nearby rivers. The study reaches and gauging stations (*) are indicated.

FIGURE 2. Mean Monthly Discharge (m^3/s) of the Marias River upstream (near Shelby at gauging station 06099500) and downstream (south of Chester at gauge 06101500) in 1946, prior to the installation of the Tiber Dam.

FIGURE 3. Annual Mean Discharge (m^3/s) of the Marias River upstream and downstream from the Tiber Dam for the period 1956 to 1990. The Dam was completed in 1956.

FIGURE 4. Flood return (recurrence) interval analyses for the Marias River. Graph A (top) plots peak discharge (maximum daily mean flows) versus return interval at the Shelby gauge, upstream from the Tiber Dam site, for the period from 1902 to 1908 and 1911 to 1993. The nine downstream points represent daily mean discharges for the nine years with the highest peak discharges at the upstream site after 1956, the completion year for the Tiber Dam. Those nine downstream values are plotted at the return interval determined for the upstream value of the same year. Graph A reveals a two-part function with a break at about the 10 year return interval. Separate regression analyses were consequently performed as represented in graphs B and C.

Graph B (middle) expands the region of Graph A from the 1 to 10 year return interval, and includes downstream points for all years after 1956. Regression lines are plotted: upstream - peak discharge = 66.6 + 255 (log (return interval)), $r^2 = 0.984$; downstream - peak discharge = 34.4 + 85.3 (log (return interval)), $r^2 = 0.503$). Upstream peak discharges for 1991 and 1980 are indicated, these were the highest peak discharge years in the past 15 years.

Graph C (bottom) plots the 10 to 100 year return interval portion of Graph A, on a normal scale which provided the maximal regression fit. A regression line is plotted for the upstream function: peak discharge = 23.1 + 34.0 (return interval), $r^2 = 0.995$).

FIGURE 5. Monthly Mean Discharges (m^3/s) upstream and downstream from the Tiber Dam, averaged for the period of 1957 through 1990, following the installation of the Tiber Dam.

FIGURE 6. Daily mean discharges (m^3/s) for the upstream and downstream reaches of the Marias River for the periods of April through September in 1964 and 1975, the years of record with the highest peak discharges, and 1980 and 1981, the two years of the 1980's decade with the highest peak discharges. For figure clarity, discharge axis scales for 1964 and 1975 have been limited to 1000 m^3/s and the arrows indicate three days for which discharges exceeded this value. Note that the discharge axes vary for the 1964 and 1975 versus 1980 and 1981 plots.

FIGURE 7. Outlines of cottonwood leaves sampled along the Marias River near the Tiber Dam. As indicated, three Populus *species occur ,* P. angustifolia, *the narrowleaf cottonwood,* P. balsamifera, *the balsam poplar, and* P. deltoides, *the prairie cottonwood. Intermediate leaf shapes indicate the occurrence of interspecific hybrids. The black bar indicates a length of 10 cm.*

FIGURE 8. Color photographs showing typical point bars of meander lobes along the Marias River, upstream (top, near Naismith) and downstream (Moffat Bridge) of the Tiber Dam on the Marias River, July 10 (upstream) and 11, 1994. Both views are directed upstream and discharges are similar. The photographs illustrate the major findings of the present study. (1) The most conspicuous difference is the (natural) occurrence of barren areas adjacent to the stream along the upstream reach versus the encroachment of grasses and shrubs right to the river's edge along the downstream reach. The barren zone sloping away from the stream is the principal site for cottonwood seedling recruitment. (2) The river upstream is turbid whereas the river downstream is clear. (3) Silt and sand has been freshly deposited along the lower (left) end of the upstream meander lobe reflecting active erosion and depositional processes, and (4) mature cottonwoods both upstream and downstream appear generally healthy. The upstream photograph also reveals the moist capillary fringe that can be

seen as a darker band extending from the stream edge, particularly in the lower left corner of the upper photograph.

FIGURE 9. Vegetation cover (%) versus distance along transects perpendicular from the river on three meander lobes upstream and downstream from the Tiber Dam on the Marias River in 1991. As further explained in the Methods section, to allow comparisons the 0 distance is an estimate of the position of the river edge when the river stage is 0.6 m above the stage at a reference discharge of 8.5 m^3/s.

FIGURE 10. Suspended material (mg/L) in the Marias River upstream and downstream from the Elwell reservoir on June 27, 1991. Values are means of three samples ± s.e..

FIGURE 11. Elevation versus distance for two transects perpendicular from the river on meander lobes upstream and downstream of the Tiber Dam on the Marias River. the 0.0 elevation is an estimate of the river stage at a flow of 8.5 m^3/s and consistent with Figure 8, the 0 distance is an estimate of position of the river edge when the river stage is 0.6 m above the baseline elevation.

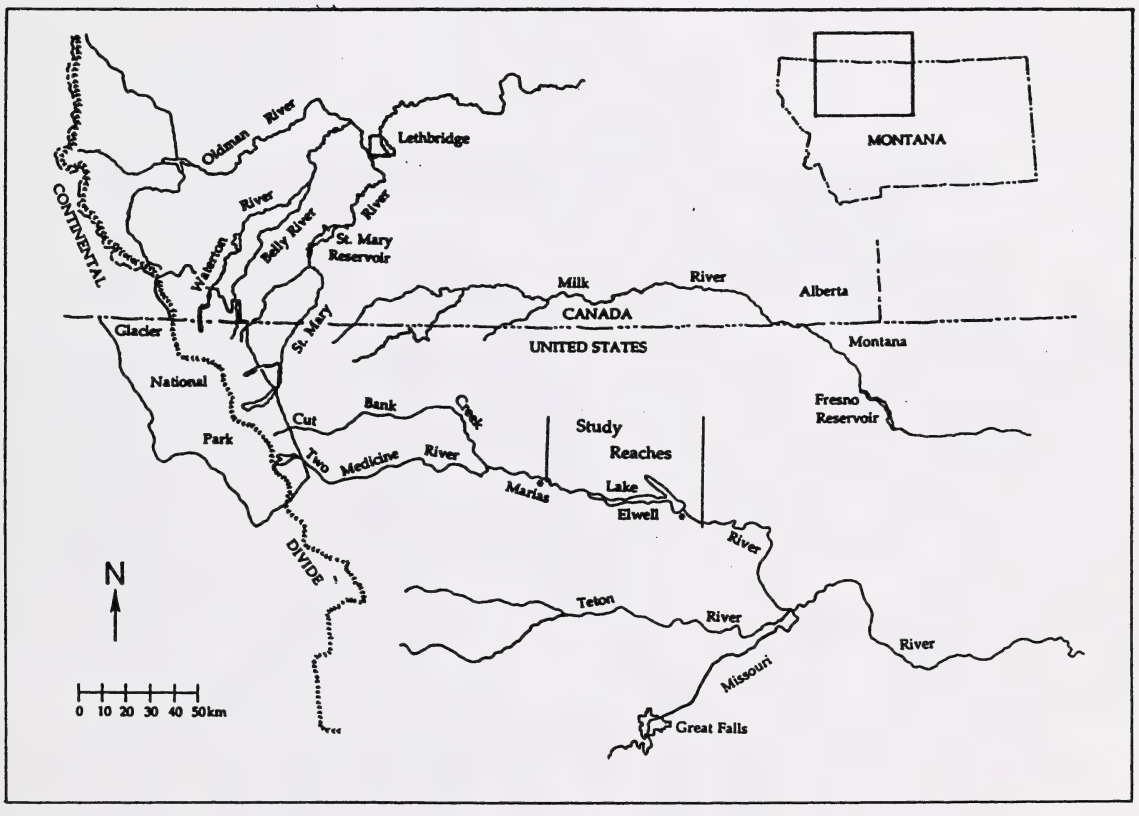
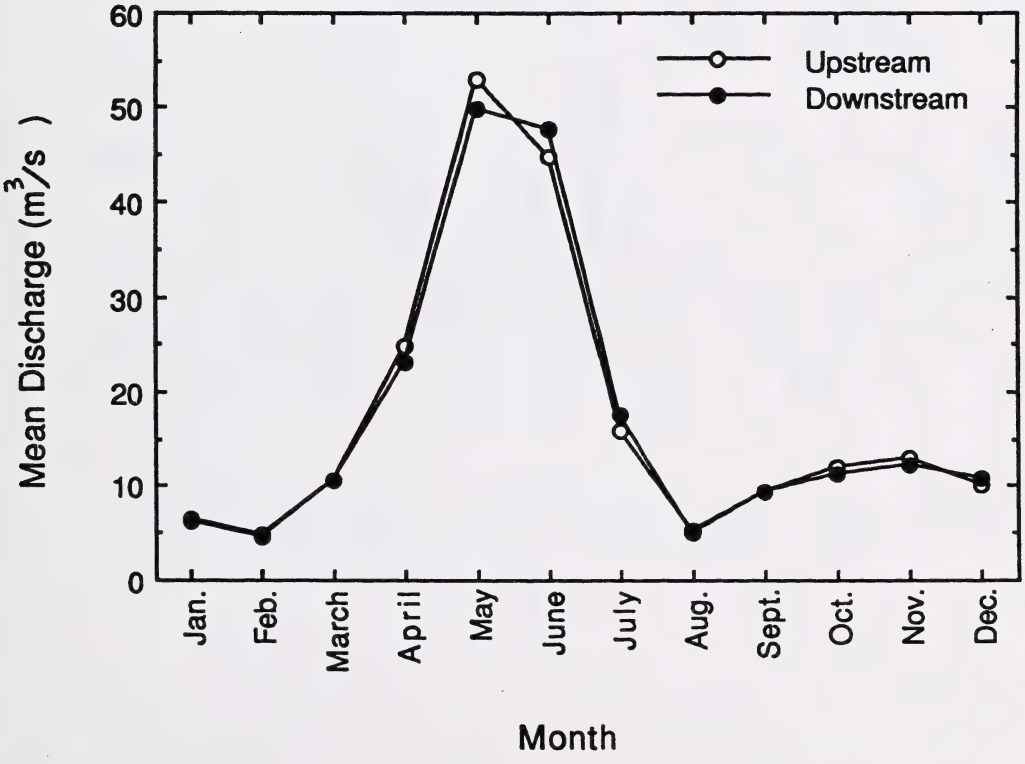

MONTANA
Oldman River
Lethbridge
CONTINENTAL DIVIDE
Waterton River
Belly River
St. Mary River
St. Mary Reservoir
Milk River
Alberta
CANADA
UNITED STATES
Montana
Glacier National Park
St. Mary
Cut Bank Creek
Two Medicine River
Study Reaches
Marias
Lake Elwell
Fresno Reservoir
Teton River
Missouri River
Great Falls
N
0 10 20 30 40 50km

Figure 2


Mean Discharge (m^3/s)
60
50
40
30
20
10
0
Upstream
Downstream
Jan.
Feb.
March
April
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Month

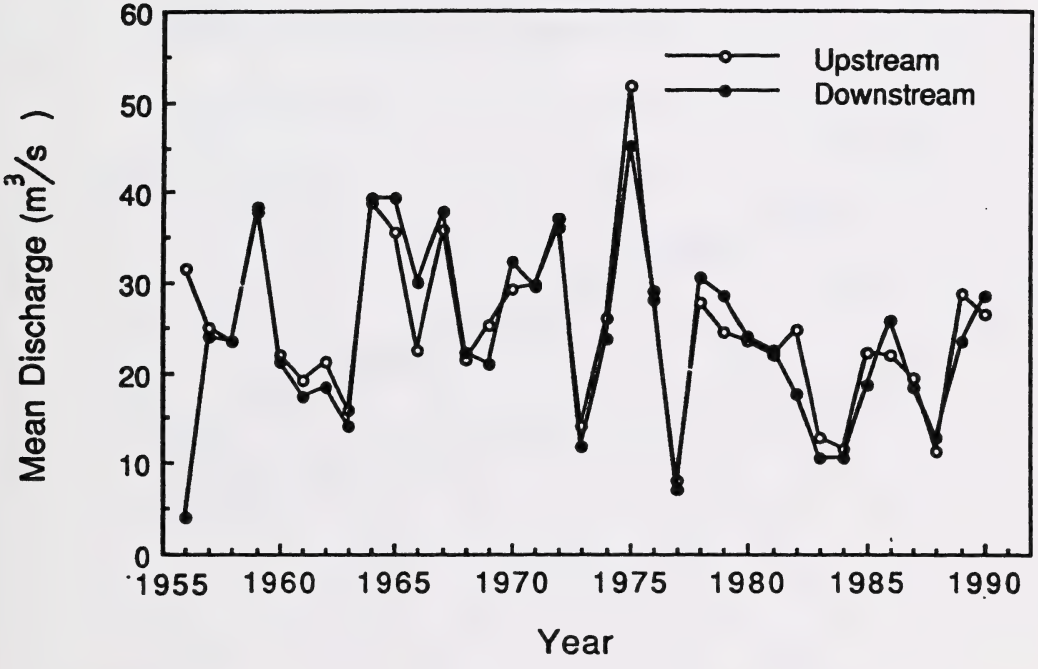

Upstream
Downstream
Mean Discharge (m^3/s)
60
50
40
30
20
10
0
1955
1960
1965
1970
1975
1980
1985
1990
Year

Figure 4

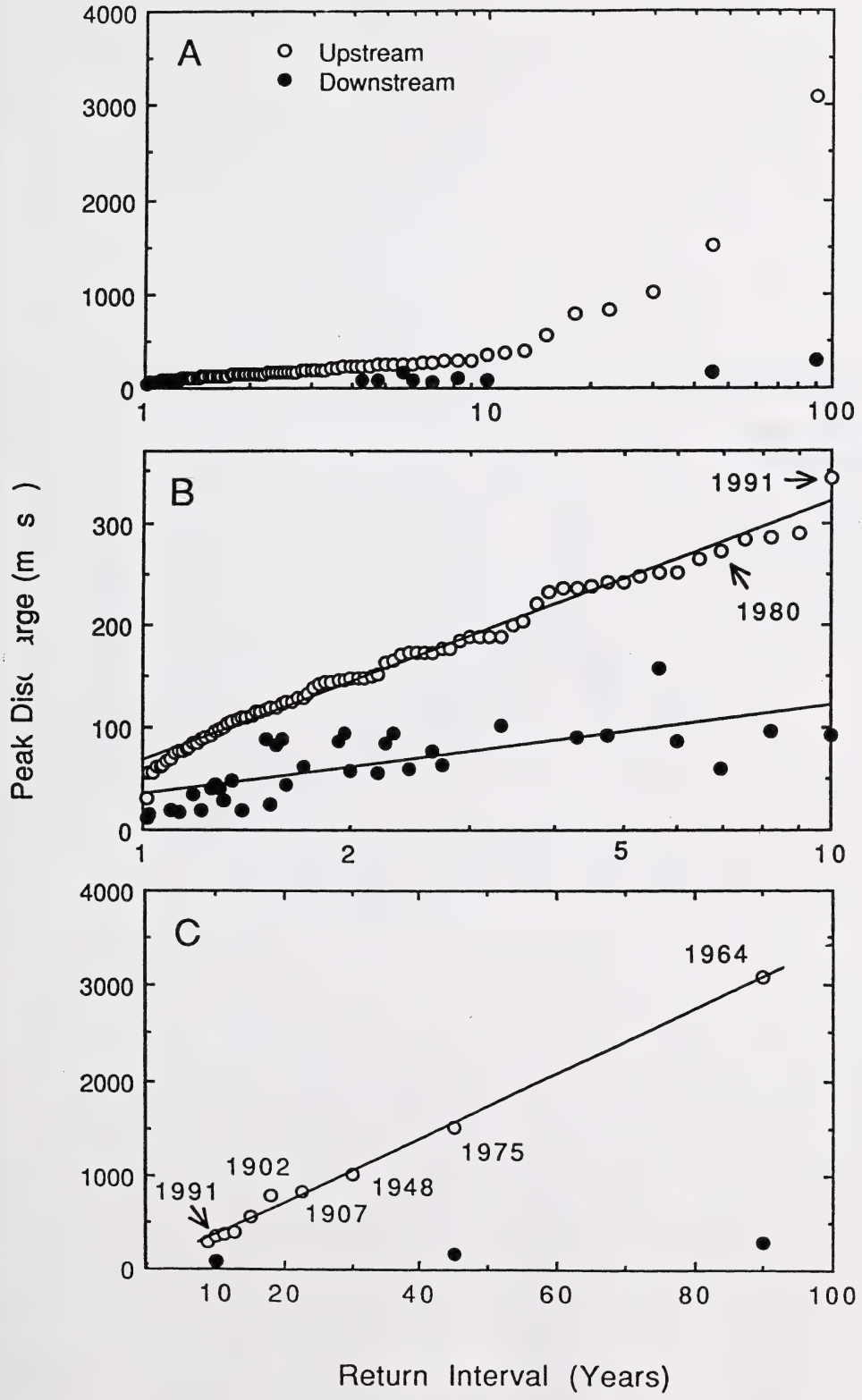

A
Upstream
Downstream
4000
3000
2000
1000
0
1
10
100
B
1991
1980
300
200
100
0
1
2
5
10
C
1964
1975
1948
1907
1902
1991
4000
3000
2000
1000
0
10
20
40
60
80
100
Peak Disc arge (m s)
Return Interval (Years)

Figure 5

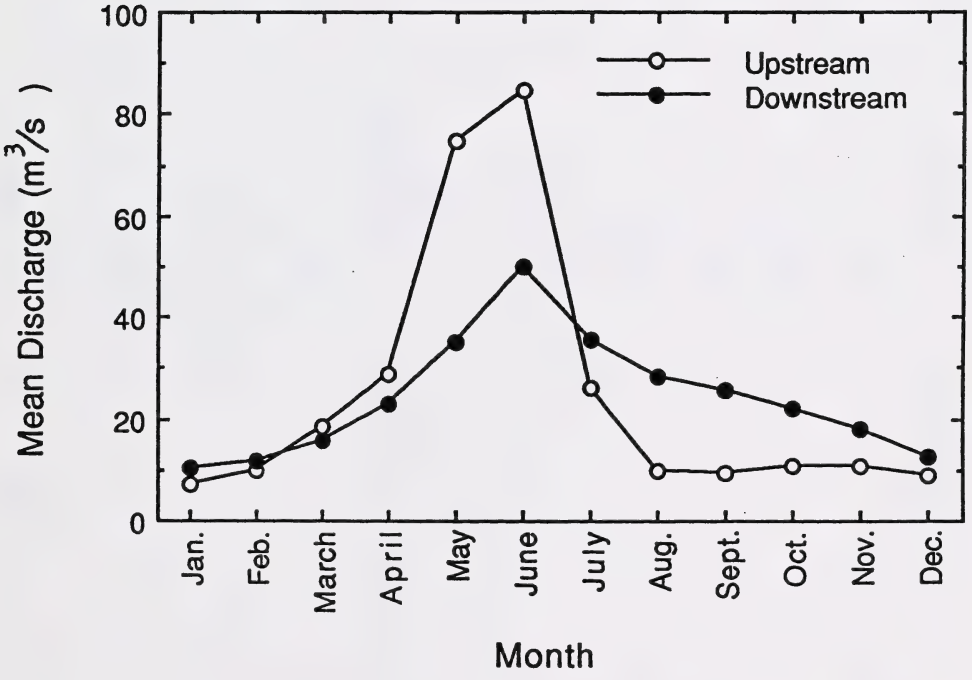

Mean Discharge (m^3/s)
100
80
60
40
20
0
Upstream
Downstream
Jan.
Feb.
March
April
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Month

Figure 6

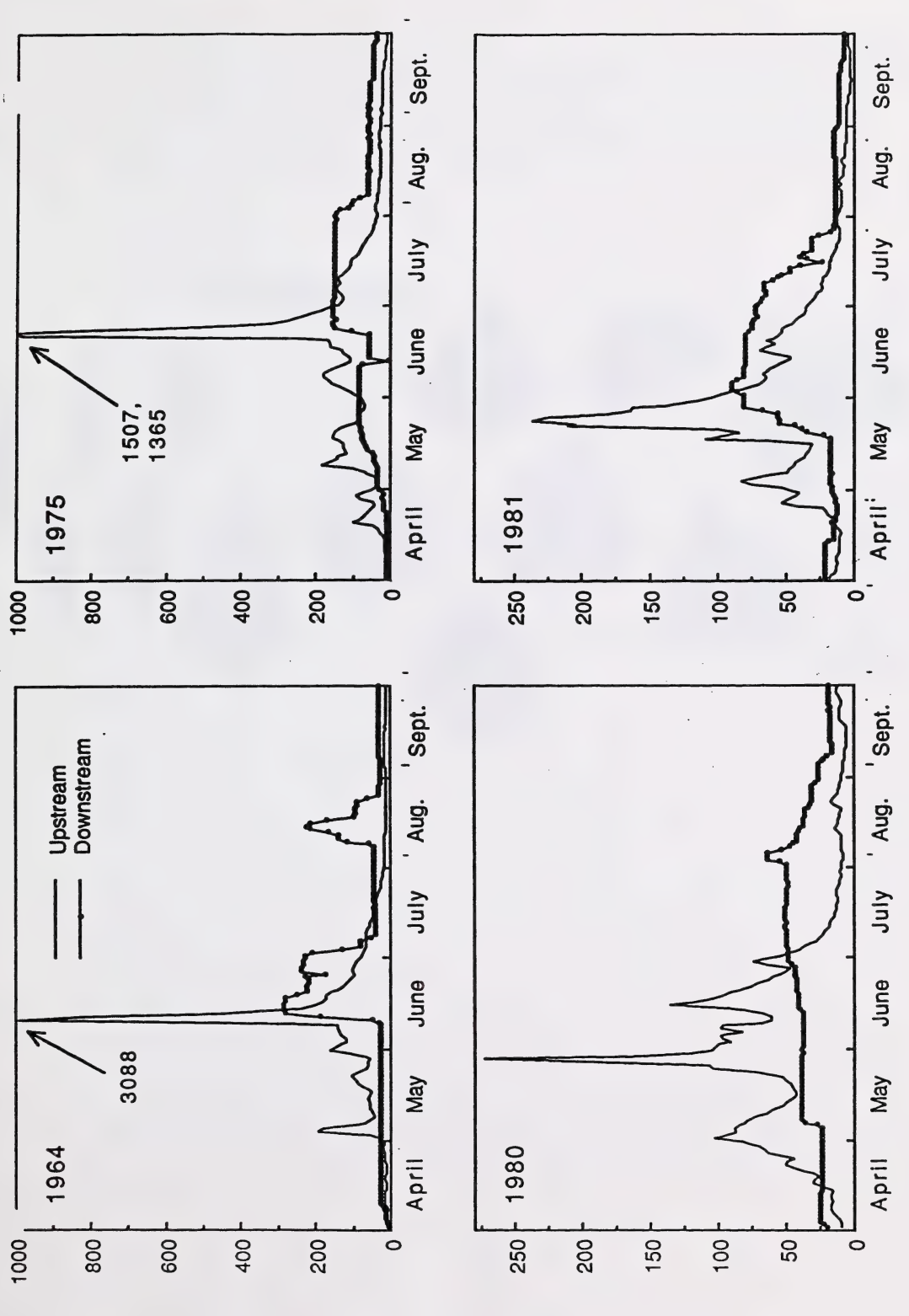
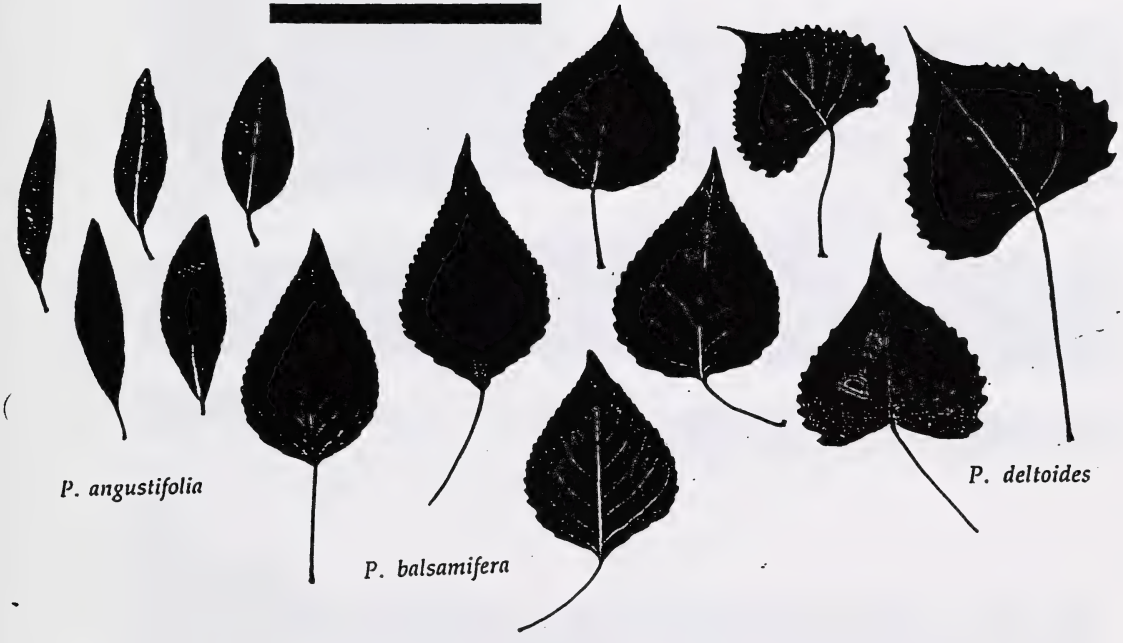

1964
3088
Upstream
Downstream
1975
1507,
1365
1980
1981
April
May
June
July
Aug.
Sept.
0
200
400
600
800
1000
50
100
150
200
250
Discharge (m³/s)

Figure 7



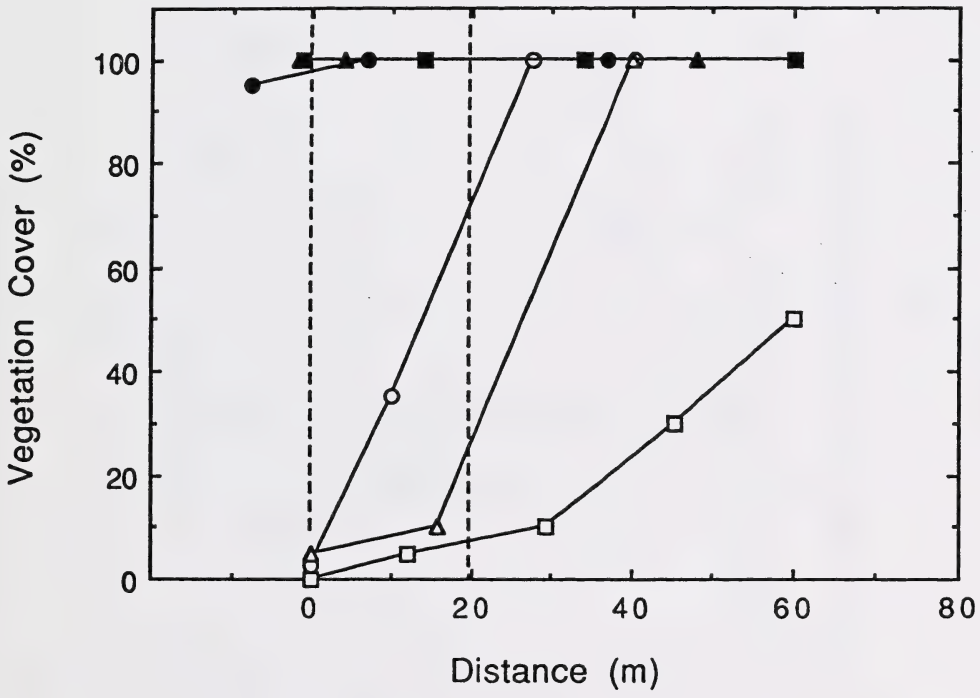
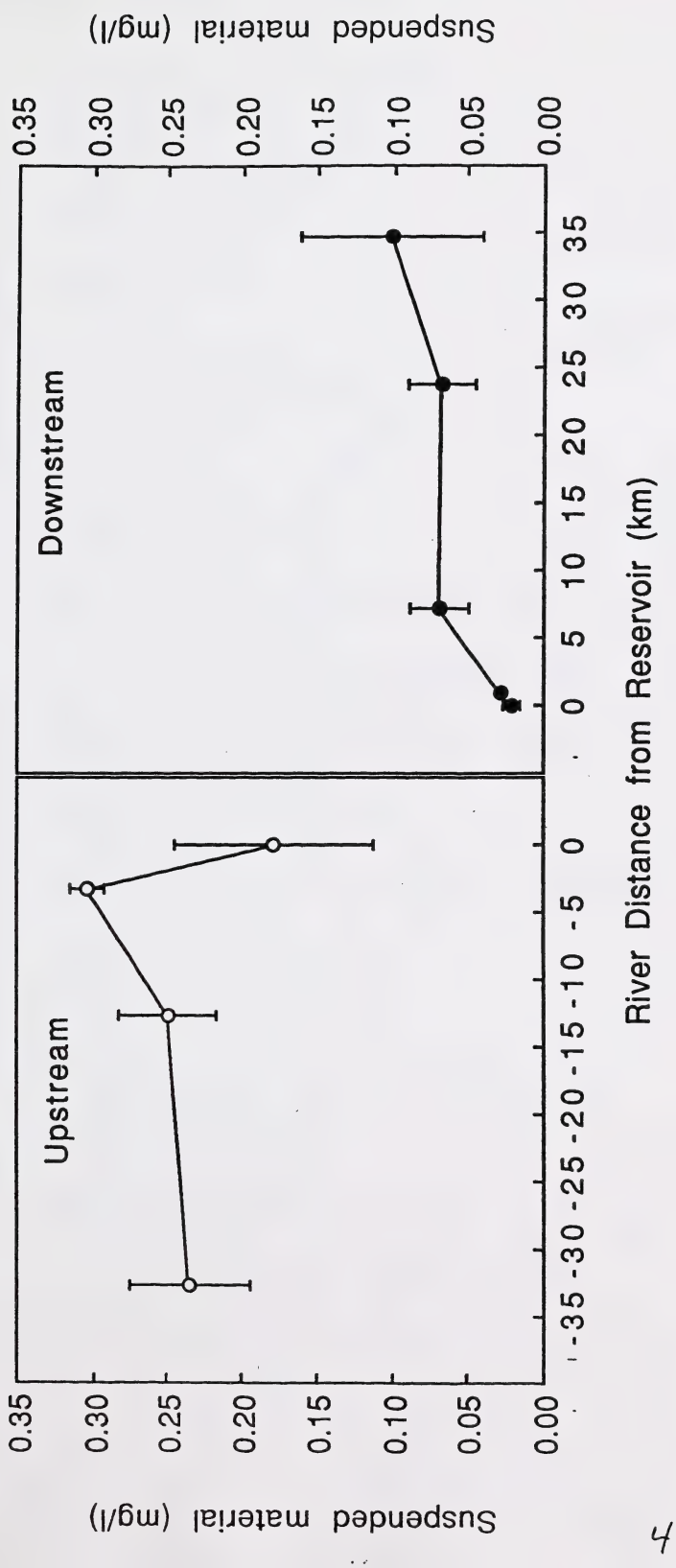
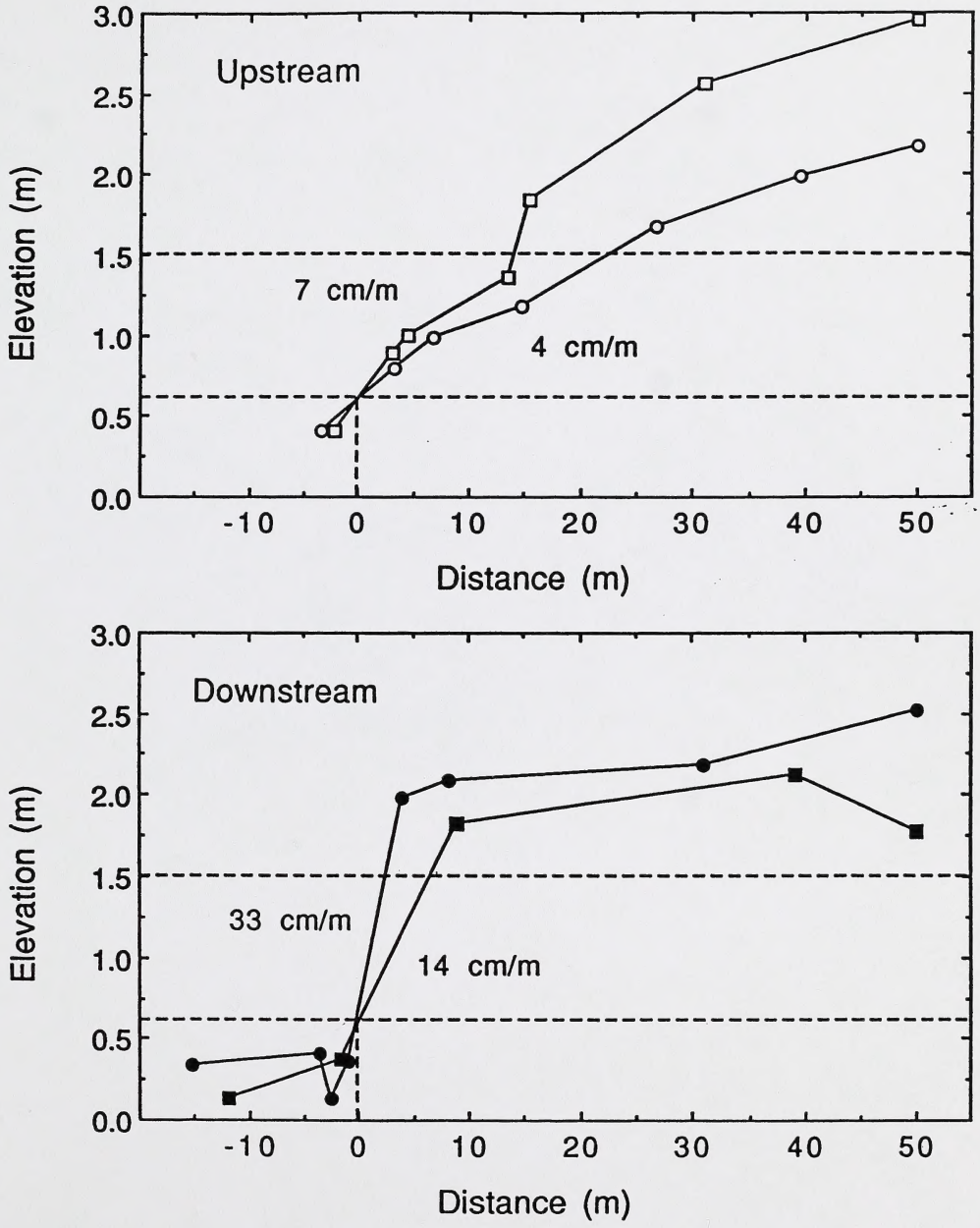

Vegetation Cover (%)
100
80
60
40
20
0
0
20
40
60
80
Distance (m)

Figure 10


Suspended material (mg/l)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Upstream
Downstream
-35 -30 -25 -20 -15 -10 -5 0 0 5 10 15 20 25 30 35
River Distance from Reservoir (km)


Upstream
7 cm/m
4 cm/m
Elevation (m)
Distance (m)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-10
0
10
20
30
40
50
Downstream
33 cm/m
14 cm/m
Elevation (m)
Distance (m)

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